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# 1988

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BOEHLERT, G. W. 1988. Seamount acoustic scattering: nocturnal emissions or organismal activities? Eos Trans. Am. Geophys. Union 69(49):1619-1628.. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8814

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BOVENG, P., D. P. DeMASTER, and B. S. STEWART. 1988. Dynamic response analysis. III. A consistency filter and application to four northern elephant seal colonies. Mar. Mammal Sci. 4(3):210-222.. . . . . . . . . . . . . . 8817

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BUTLER, J. L., and D. PICKETT. 1988. Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 86:163-167.. . . . . . . . . . . . . . . . . . . . . . . . . . . 8819

CHESS, J. R., S. E. SMITH, and P. C. FISCHER. 1988. Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. Calif. Coop. Oceanic Fish. Invest. Rep. 29:129-136. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8820

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HIGHTOWER, J. E., and G. D. GROSSMAN. 1988. Status of the tilefish, *Lopholatilus chamaeleonticeps*, fishery off South Carolina and Georgia and recommendations for management. Fish. Bull., U.S. 87:177-188. . . . . . . . . . . 8831

HOBSON, E. S., and J. R. CHESS. 1988. Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California. Fish. Bull., U.S. 86(4):715-743. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8832

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HUPPERT, D. D. 1988. Marine fishery regulations in the U.S. and the role of economic analysis. *In* J. W. Milon (ed.), Marine fishery allocations and economic analysis, pp. 1-9. Southern Rural Development Center No. 26, Mississippi State Univ., MS. . . . . . . . . . . . . . . . . . . . 8836

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LASKER, R. 1988. Food chains and fisheries: an assessment after 20 years. *In* B. J. Rothschild (ed.), Toward a Theory on Biological-physical Interactions in the World Ocean, pp. 173-182. Kluwer Academic Publishers. . . . . . . . . . 8839

LASKER, R. 1988. Studies on the northern anchovy; biology, recruitment and fishery oceanography. Studies on Fisheries Oceanography. Edited by the Japanese Society of Fisheries Oceanography, pp. 24-42. . . . . . . . . . . . . . . . 8840

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# GEOGRAPHIC VARIATION IN TOOTH MORPHOLOGY AND DENTINAL PATTERNS IN THE SPINNER DOLPHIN, *STENELLA LONGIROSTRIS*

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## Abstract

Sixteen tooth characters were analyzed in 277 specimens of spinner dolphins (*Stenella longirostris*) from the eastern tropical Pacific to determine whether the characters were associated with size of the animal, species-stock membership or geographic location. The tooth characters included 5 continuous measurements and 11 qualitative variables. Statistical analyses of the characters included two-way ANOVA tests which assessed continuous measurement variables for differences based on stock membership, latitude and longitude of collection or whether the animal was collected north or south of the equator. Principal component analyses combined factors of continuous variables with those of qualitative variables into components which were used as variables in further analyses. Discriminant analyses were performed using continuous variables alone and using principal components as potentially discriminating variables. Results showed that tooth differences were not associated with size but significant differences were found in some tooth variables with stock membership, incremental changes in latitude and whether the animal was collected north or south of the equator. A discriminant function, containing only tooth length, correctly classified 67% of northern and 78% of southern animals according to location of collection north or south of the equator.

Key words: spinner dolphin, *Stenella longirostris,* tooth characters, geographic variation.

A number of dolphin populations in the eastern tropical Pacific are caught incidentally by tuna seiners during fishing operations. One such species, the spinner dolphin, *Stenella longirostris,* includes a number of population stocks: the eastern spinner dolphin, northern and southern whitebelly spinner dolphin, Costa Rican spinner dolphin and Hawaiian spinner dolphin (Perrin *et al.* 1979, 1985). Stock membership is determined at sea by government observers using distinguishing criteria of snout and dorsal fin shape and overall body form. Another recognized category, 'unidentified,' are animals with an intergrade color pattern and which were collected where the ranges of the northern whitebelly spinner and the eastern spinner dolphin stocks overlap (Perrin and Henderson 1984).

In previous studies, researchers have used variability in color pattern, skull features and dorsal fin shape to characterize geographic variation in dolphins. Perrin (1972) described variations in color pattern in spinner dolphins and Perrin *et al.* (1979) studied variation in spotted dolphins (*S. attenuata*) and spinner dolphins north and south of the equator using skull features. Schnell *et al.* (1982) used skull features and total body length to study geographic variation in spotted and spinner dolphins and later (Schnell *et al.* 1985) found cranial morphometric differences between whitebelly and eastern spinner dolphin stocks compared from throughout the range. They also found strong cranial morphometric differences between samples of whitebelly spinner dolphins collected north or south of the equator. Tooth differences such as tooth width were found to be important by Douglas *et al.* (1984) who used multivariate analysis techniques on skull and tooth characters of spotted dolphins. They found a sharp demarcation between the characters of inshore and offshore populations, with tooth width as the most distinguishing variable. Walker (1981) also found tooth width the best character for distinguishing populations of *Tursiops truncatus.*

The purpose of this paper is to present results of statistical comparisons of morphometric and other morphological differences in teeth from different spinner dolphin populations. Comparisons were made to determine if these differences are associated with dolphin stock membership or geographic location.

## METHODS AND MATERIALS

*The sample*—In a separate study to estimate the age structures of the spinner dolphin populations in the eastern Pacific, teeth of female spinner dolphins were prepared and read to obtain age estimates (Myrick and Akin, in prep.). All samples were taken from the mid-portion of the lower-left jaw. Teeth in this region are uniform and least likely to be worn, broken or crowded.

Preparation technique was identical for all specimens. Preparation included decalcifying, sectioning, staining and mounting the sections on glass slides (Myrick *et al.* 1983). The 25-$\mu$m thick sections were taken longitudinally, from the tooth apex to the base, through the most central portion of the tooth. Stained central sections revealed all growth layers and other markings and patterns in the dentine as well as a readable portion of cementum. Age estimates of dolphins were obtained by counting units of associated layers or growth-layer-groups (GLGs, Myrick 1980) in the tooth sections. GLGs, deposited at the rate of one per year, provide an age estimate of the animal.

Three hundred fifty-one tooth specimens were non-randomly selected and examined for variation in tooth characters. (The sample was stored alphabetically by collector's name and was selected casually across the alphabet.) Because delphinid teeth increase in length for the first 3–4 yr (van Utrecht 1981), teeth with fewer than four GLGs were removed from the sample and not considered in this study.

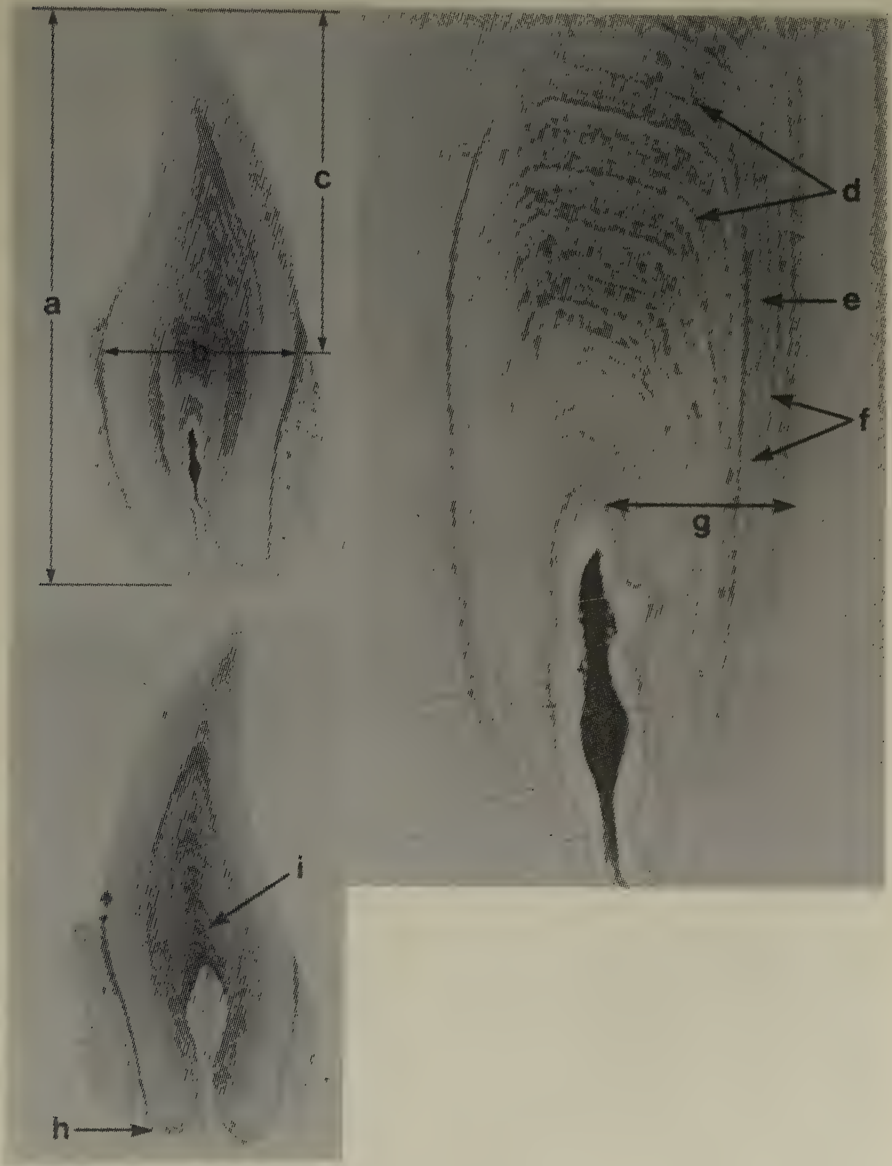

*Figure 1.* Recorded tooth variables. (a) tooth length, (b) width, (c) height of crown, (d) angular-shaped GLGs in crown, (e) paired lines, (f) crenulate lines, (g) GLG density, (h) truncated base and (i) triangular GLGs in crown.

*The variables*—The remaining 277 specimens were analyzed using 16 tooth characters, including various continuous and qualitative variables (Figs. 1 and 2). The continuous variables, which were taken in micrometer units on each tooth, were length (a), measured as a vertical line from the apex to the base

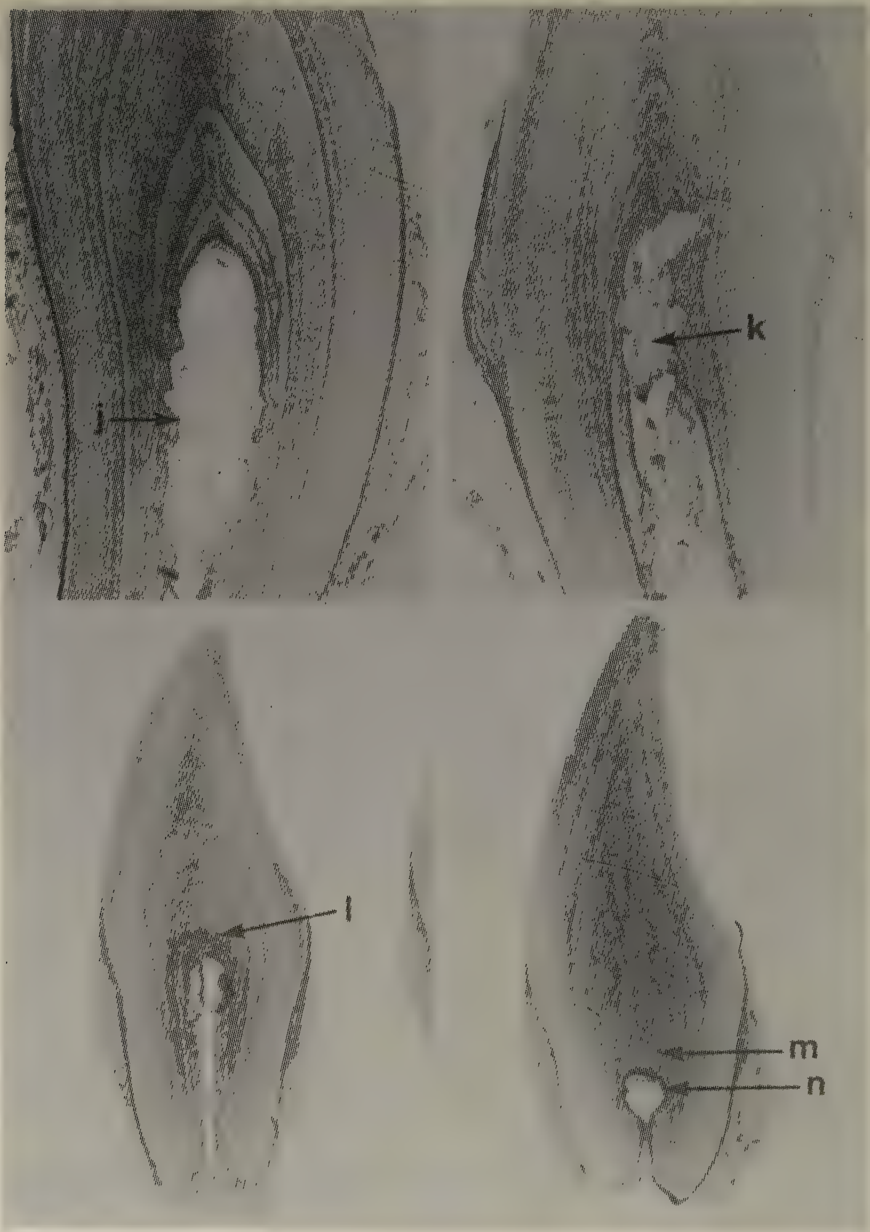

*Figure 2.* Additional variables noted. (j) crenulated pulp cavity margin, (k) globular 'pearls' in pulp cavity, (l) flat-topped pulp cavity, (m) curved GLGs in crown and (n) key-shaped pulp cavity.

*Table 1.* Results of two-way ANOVA tests comparing tooth measurement characters for a sample of spinner dolphin teeth. Comparisons were made by stock membership and geographic location.

| | | *F*-values | | |
|---|---|---|---|---|
| Character | Stock | Long | Lat | NS |
| Length | 3.14* | 1.73 | 2.90* | 7.39* |
| | $P$ = (0.0451) | (0.1152) | (0.0146) | (0.0070) |
| Width | 3.57* | 0.42 | 0.76 | 0.23 |
| | (0.0296) | (0.8655) | (0.5810) | (0.6300) |
| Crown height | 0.85 | 1.70 | 1.90 | 3.87* |
| | (0.4278) | (0.12) | (0.0944) | (0.0500) |
| Width/length | 1.62 | 1.13 | 2.18 | 4.89* |
| | (0.1995) | (0.343) | (0.0571) | (0.028) |
| Crown ht./length | 7.06* | 0.23 | 0.19 | 0.67 |
| | (0.0010) | (0.9655) | (0.9661) | (0.4104) |

* $P = <0.05$ indicates significant differences.

of the tooth; width (b), measured horizontally across the widest portion of the crown dentine excluding the cement; and height of crown (c), taken as a straight-line measurement from the apex to the neck (gum-line) of the tooth perpendicular to the width. The ratio of width to length and the proportion of height of crown to length were calculated. The density of 'lines' (g) (GLG boundaries and other prominent, narrow incremental layers in the dentine) was estimated by counting the number of lines intersected by a horizontal scale projected from the top of the pulp cavity, 20 micrometer units to the right.

Qualitative variables, reported as being present or absent, included GLG patterning of paired lines (e), which are a pair of lines parallel to each other and closer together than the next line on either side and which are within but not constituting the boundaries of a GLG and crenulate lines (f), which are GLGs that are wavy rather than smooth. GLG shape in the crown was recorded as triangular (i), curved (m) or angular (d). The occurrence of very wide GLGs at the base of the tooth (the first 3 or 4 GLGs) which are truncated giving the tooth an oblate appearance was noted (h). Qualitative characters of the pulp cavity recorded were presence of flat-topped (l) or key-shaped outlines (n), crenulate margins (f) or pearl-like globular deposition patterns (k).

*The analyses*—A sequence of statistical analyses was performed to evaluate the descriptive value of the variables chosen and to allow the inclusion of both continuous and qualitative characters in the comparison tests.

Because differences in tooth measurements can be a reflection of individual growth, I used body length, an indicator of growth, to test the measurements using one-way ANOVA (Program 1V of BMDP-81; Dixon 1981).

To determine if the measurement differences were characteristic of particular dolphin stocks or localities, two-way ANOVA (BMDP 2V) tests were performed on continuous variables. The categories compared were eastern spinner, whitebelly spinner and unidentified spinner dolphins. Collection localities were categorized by 10-degree increments in longitude, 5-degree increments in latitude and sites from either north or south of the equator.

Principal component analyses were used to evaluate overall variation and to allow inclusion of qualitative variables with the continuous variables. The three main principal components found incorporated a combination of all continuous measurement data with the four retained qualitative variables of line density, paired lines, crenulate lines and GLG shape.

Step-wise discriminant analyses (BMDP 7M) were performed to identify functions that would correctly classify specimens into groups of (1) previously-assigned species-stocks, (2) collection localities north or south of the equator, (3) latitude or (4) longitude.

Discriminant analyses were performed with a variety of variable combinations entering the calculations. Initially, all variables (continuous and qualitative) were entered, then only continuous variables were entered. Finally, principal components were entered as the potentially discriminating variables.

## Results

The basic dentinal shapes and patterns appear distinctive but there is much variation and many degrees of differences. After quantifying and analyzing these differences statistically, however, the number of useful distinguishing characters was quickly reduced.

ANOVA tests, comparing differences in the measurement characters of length, width, crown height, width/length and crown height/length, showed no differences with body length but showed significant differences in some other comparisons (Table 1). Tooth length, width and crown height/length differed significantly ($P < 0.05$) between the species stocks. Tooth length differed by latitude, and tooth length, crown height and width/length differed between specimens from north or south of the equator. No significant differences were found in any measurement variable when compared for differences in longitude.

General characteristics of significant continuous variables are presented in Table 2, sections A, B and C. Examining tooth differences by stock membership indicated that the average whitebelly spinner tooth was longer and wider than the average eastern spinner dolphin tooth. Spinner dolphins collected south of the equator had longer teeth and greater crown height than northern spinner dolphins. Northern spinner dolphins had shorter, broader teeth as shown by the higher width/length ratios. Comparing spinner dolphin teeth by latitude, the average tooth length was greatest in animals collected from 5 degrees south to the equator.

Step-wise discriminant analysis, performed with various combinations of input variables, correctly classified the same percentages of specimens when all variables (qualitative and continuous) were entered and when only continuous variables were entered. This suggests that the qualitative variables chosen, while possibly being locally distinctive, do not add more power to the discriminating functions than the use of measurements alone.

Discriminant analysis was most successful in separating specimens as to whether they were collected north or south of the equator. Separation of stocks or

*Table 2.* Means, standard deviations and ranges of tooth variables found to be significant in two-way ANOVA analyses.

| | Stock | $\bar{x}$ | SD | Range |
|---|---|---|---|---|
| A. Comparison of variables by dolphin stock membership | | | | |
| Length | Eastern | 294.1 | 31.4 | 220–391 |
| | Whitebelly | 316.1 | 35.5 | 214–392 |
| | Unidentified | 305 | 21.2 | 271–346 |
| Width | Eastern | 82.4 | 7.7 | 60–100 |
| | Whitebelly | 86.5 | 6.9 | 63–101 |
| | Unidentified | 81.5 | 8.5 | 66–95 |
| Crown ht/ length* | Eastern | 0.944 | 0.05 | 0.819–1.06 |
| | Whitebelly | 0.906 | 0.05 | 0.698–1.03 |
| | Unidentified | 0.937 | 0.04 | 0.864–1.02 |
| B. Comparison of variables by group from north or south of the equator | | | | |
| Length | Northern spinner | 302.7 | 34.2 | 214–392 |
| | Southern spinner | 329.3 | 25.6 | 275–380 |
| Crown height | Northern spinner | 192.8 | 22.3 | 100–250 |
| | Southern spinner | 203.8 | 16.6 | 150–235 |
| Width/length | Northern spinner | 0.281 | 0.04 | 0.184–0.446 |
| | Southern spinner | 0.260 | 0.02 | 0.226–0.293 |
| C. Comparisons of tooth variables by latitude: all dolphin stocks | | | | |
| | Latitude | $\bar{x}$ | SD | Range |
| Length | ≥−5 degrees | 323.5 | 18.1 | 290–346 |
| | 0 | 334.5 | 27.6 | 275–380 |
| | 5 | 315 | 33.6 | 214–382 |
| | 10 | 303.9 | 31.5 | 214–392 |
| | 15 | 294.3 | 36.2 | 220–391 |
| | 20 | 293 | 12.2 | 285–307 |

* Data converted by an arcsine transformation.

separation by longitude or latitude of collection was marginally successful (44 to 71% correctly classified).

A single variable, tooth length ($L$) was the most important character in the discriminant analysis. Specimens of all stocks combined (67.44% of northern and 75.9% of southern) were correctly classified as having been collected north or south of the equator with a discriminating function of tooth length; for northern specimens, the classification function is $Z1 = .27488L - 42.37716$ and for southern, $Z2 = .30184L - 50.95422$. (To use this function, calculate the scores $Z1$ and $Z2$. The specimen goes into the group for which the classification function is largest.) The largest percentage of correct classifications was within four degrees north of the equator.

## DISCUSSION

Teeth of spinner dolphins from the eastern Pacific showed more variation in tooth morphometrics than in pattern or pulp cavity characters. Pattern and pulp cavity characters may be distinctive enough that they might be useful as identifying characteristics of a population. However, sample sizes were not large enough to demonstrate this in this study.

Although tooth morphometrics were shown by ANOVA tests to differ with stock designation, there is overlap of the variable ranges, and separation was incomplete.

Variation in tooth morphology was strongly associated with incremental increases in latitude for northern and southern spinner dolphins. There is evidence for geographic variation in tooth length between northern and southern spinner dolphin populations when combining eastern spinner dolphin and northern and southern whitebelly spinner dolphin stocks. Similarly, northern and southern whitebelly spinner dolphins show variation in tooth length when tested alone.

Perrin *et al.* (1979), utilizing skull features and color pattern, found that the southern whitebelly spinner dolphins were clearly different from the northern whitebelly spinner dolphins. Schnell *et al.* (1985) compared variation in cranial characters of whitebelly spinner dolphins and found differences between northern and southern populations. He also found cranial differences between the northern and southern spinner dolphin with eastern spinner, northern and southern whitebelly spinner stocks combined (Schnell *et al.* 1985). Results in this study are similar; differences are latitudinal, north and south of the equator, whether all spinner dolphin stocks or whitebelly spinner dolphins only are compared.

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Alec MacCall gave vital statistical advice during the course of the analyses. A. C. Myrick, W. F. Perrin, A. Dizon and D. DeMaster read the manuscript and offered useful suggestions for its improvement. J. Michalski made editorial suggestions.

## Literature Cited

Dixon, W. J. 1981. BMDP statistical software. Department of Biomathematics, University of California, Los Angeles.

Douglas, M. E., G. D. Schnell and D. J. Hough. 1984. Differentiation between inshore and offshore spotted dolphins in the eastern tropical Pacific Ocean. Journal of Mammalogy 65:375–387.

Myrick, A. C., Jr. 1980. Examination of layered tissues of odontocetes for age determination using polarized light microscopy. Pages 105–112 *in* W. F. Perrin and A. C. Myrick, Jr., eds. Age determination of toothed whales and sirenians. Report of the International Whaling Commission Special Issue 3.

Myrick, A. C., Jr., A. A. Hohn, P. A. Sloan, M. Kimura and D. D. Stanley. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from teeth. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-30. 17 pp.

Perrin, W. F. 1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fishery Bulletin., U.S. 70:983–1003.

Perrin, W. F., and J. R. Henderson. 1984. Growth and reproductive rates on two populations of spinner dolphins, *Stenella longirotis*, with different histories of exploration. Report of the International Whaling Commission Special Issue 6:417–430.

PERRIN, W. F., P. A. SLOAN AND J. R. HENDERSON. 1979. Taxonomic status of the 'Southwestern Stocks' of spinner dolphin *Stenella longirostris* and spotted dolphin *S. attenuata*. Report of the International Whaling Commission 29:175–184.

PERRIN, W. F., M. D. SCOTT, G. J. WALKER AND V. L. CASS. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Technical Report NMFS 28.

SCHNELL, G. D., M. E. DOUGLAS AND D. J. HOUGH. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Southwest Fisheries Center Administrative Report LJ-82-15c. 213 pp.

SCHNELL, G. D., M. E. DOUGLAS AND D. J. HOUGH. 1985. Further studies of morphological differentiation in spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Southwest Fisheries Center Administrative Report LJ-85-04c. 30 pp.

VAN UTRECHT, W. L. 1981. Comparison of accumulation patterns in layered dentinal tissue of some odontoceti and corresponding patterns in baleen plates and ear plugs of Balaenopteridae. Beaufortia 32:111–122.

WALKER, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern north Pacific. Southwest Fisheries Center Administrative Report LJ-81-03c. 54 pp.

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# *PANDEA CYBELES,* A NEW MEDUSA FROM THE SARGASSO SEA (COELENTERATA: ANTHOMEDUSAE: PANDEIDAE)

Angeles Alvariño

*Abstract.*—A new medusa is described and illustrated. It is compared to related species in the genus, *Pandea conica* (Quoy & Gaimard, 1827) and *Pandea rubra* Bigelow, 1913. It differs from those species in the proportions of the umbrella and its conical process, number of ribs on the umbrella, number of marginal tentacles, ocelli on the basal bulb of tentacles, and the large size of the stomach. The diagnostic characteristics of these species and *Pandea cybeles* are compiled in a table. Information is included on the distribution of the species throughout the world.

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The genus *Pandea* Lesson, 1843, includes two valid species, *Pandea conica* (Quoy & Gaimard, 1827) and *Pandea rubra* (Bigelow, 1913. Mayer (1910) recognized five species of Pandeidae: *Pandea conica* (Quoy & Gaimard, 1827), *P. saltoria* (Sars, 1835), *P. minima* von Lendenfeld, 1884, *P. violacea* Agassiz & Mayer, 1899, and *P. maasi* Maas, 1904.

According to Kramp (1965) *P. maasi* is a synonym of *Euphysa flammea* (Linko, 1905); *P. minima* and *P. violacea* are juvenile stages of indeterminable Tiaridae, placing also *P. violacea* under *Merga violacea* (Agassiz & Mayer, 1899); and *P. saltoria* is a species of *Aglantha.*

During the Sargasso Sea Biowat cruise on the R/V *Knorr* in Apr 1975, plankton collections were obtained, and some specimens of Medusae, Siphonophora, and Ctenophora were kindly sent to me by Michael Latz (Department of Biological Sciences, University of California, Santa Barbara) for identification. The medusae included three specimens of a new species of *Pandea,* described below.

### *Pandea cybeles,* new species
### Figs. 1, 2

*Material.*—NE Sargasso Sea, Biowat Cruise of R/V *Knorr,* Apr 1975, from tows with Tucker ½ m net with 333 μm mesh: Sta 240, 34°53.22′N, 70°06.01′W, ca. 100 m depth, 20 Apr 1975, holotype, USNM 77473.—Sta 231, 33°55.74′N, 69°59.11′W, ca. 1 m depth, 19 Apr 1975, paratype, USNM 77474. A third specimen from Sta 230, 33°55.74′N, 69°59.11′W, ca. 1 m depth, 19 Apr 1975, was left at the University of California, Santa Barbara.

*Description.*—Umbrella bell-shaped, slightly higher than wide (heights 18, 20 and 25 mm, widths 14.5, 16.3 and 20 mm respectively), with conical apical process about 5 mm long (measurements included in total height) in largest medusa (Fig. 1). Exumbrella with ridges reaching from tip of apical process to each marginal tentacle, alternating with grooves running from tip of apical process to spaces between tentacles at edge of umbrella. Crest of each ridge with thin whitish band, probably formed by rows of nematocysts. The four wide radial canals with rough margins. Circular or ring canal simple, about half width of radial canals, with smooth margins (Fig. 1). Centripetal canals lacking. Velum narrow.

Marginal tentacles about 40, 10 at each space between perradii, long, of same size, hollow. Base of tentacle with thick conical laterally compressed bulb or spur clasping margin of umbrella. Abaxial spur of each tentacle having 1 red ocellus.

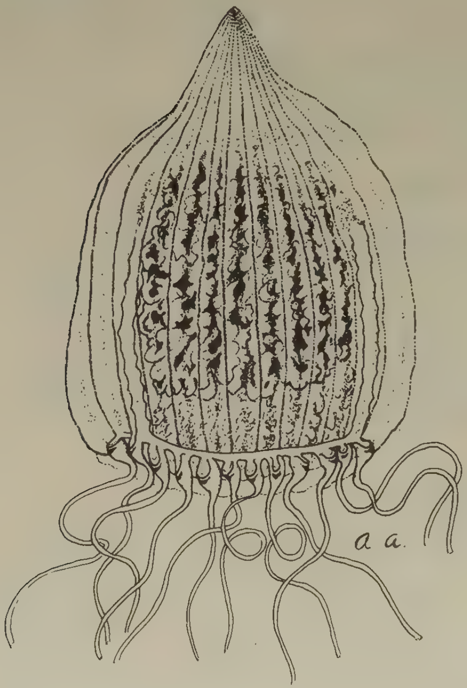

Fig. 1. *Pandea cybeles*, habitus.

Stomach large, completely filling subumbrellar cavity, attached for about ⅓ of its length to subumbrella perradii.

Mouth with 4 perradial lips deeply and complexly folded, with crenulated edges, reaching border of umbrella.

Gonads extending over interradial and perradial zones, completely covering stomach, forming irregular network of sinuous ridges and pits, latter corresponding to internal ovular formations (Fig. 2B).

Color of stomach, mouth, gonads, and border of umbrella pinkish, with light purple and violet tones. Thick jelly umbrella and conical apical process, crystal clear with violet tones, revealing darker tones of stomach and gonads within.

*Etymology.*—Named after Cybele, goddess of nature.

*Remarks.*—Differential morphological characteristics of *Pandea cybeles, P. conica,* and *P. rubra* are given in Table 1.

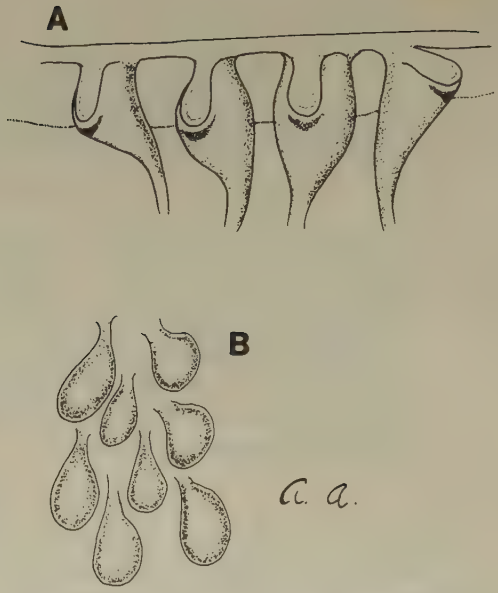

Fig. 2. *Pandea cybeles:* A, Detail of bulbs in marginal tentacles; B, Detail of internal ovular formations in gonads.

*Pandea cybeles* differs from *P. conica* in the proportion of length to width of the umbrella, the number of ribs, the number of marginal tentacles, and the size of the stomach.

*Pandea cybeles* differs from *P. rubra* in having a conical apical process of the umbrella, and ribs and nematocyst tracks on the umbrella, all of which structures are absent in *P. rubra.* The circular canal is broader in *P. rubra* than in *P. cybeles.* The number of marginal tentacles is different in the two species, and *P. rubra* does not have ocelli on the basal bulb of the tentacles.

The stomach of *P. rubra* reaches to half the length of the subumbrellar cavity; in *P. conica* it occupies about ⅓ or ½ of the length of the subumbrellar cavity, whereas in *P. cybeles* it fills completely the subumbrellar cavity, reaching the margins of the umbrella.

Differences between *Pandea rubra* and *Pandea cybeles* are obvious and do not require further discussion. However, *Pandea*

Table 1.—Principal differential characteristics of the species of *Pandea* and the new species.

| Characteristics | *Pandea conica* (Quoy & Gaimard, 1827) | *Pandea rubra* Bigelow, 1913 | *Pandea cybeles*, n. sp. |
|---|---|---|---|
| Umbrella | Bell barrel-shaped, about twice as high as wide, jelly fairly thick, with apical process | Bell-shaped, as high or slightly higher than wide, with rounded summit, without apical process. Thin soft walls | Bell-shaped, slightly higher than wide, of thick jelly, with thick apical conical process |
| Umbrella size | 20–30 mm height, 10–15 mm wide | 30–40 mm height up to 75 mm | 18–25 mm height and 14.5–20 mm wide |
| Velum | Narrow | Narrow | Narrow |
| Apical conical process | Conical at summit, with apical ectodermal thickening | Not present | Present, long conical ectodermal thickening at top of umbrella |
| Ribs and ridges | 16 or in the 20's. Exumbrellar nematocyst ribs | No ribs or exumbrellar nematocyst tracks | Present 40 exumbrellar ribs with nematocyst band at crest edge, extending from tip of conical process to edge of umbrella |
| Radial canals | 4 broad, smooth or jagged | 4 broad with wavy or jagged outlines | 4 broad with jagged outline |
| Circular canal | Narrower than radial canals, smooth outlines | Broad, with smooth outlines | Narrower than radial canals, about half width, smooth outlines |
| Marginal tentacles | 16 or in the 20's, smooth, hollow, with conical laterally compressed basal bulb, without well developed abaxial spur, with one abaxial ocellus. No rudimentary marginal tentacles | 18–24 of various sizes, hollow, smooth, with large conical basal bulb, not laterally compressed, with distinct abaxial spur clasping margin of umbrella. No ocelli. No rudimentary marginal tentacles | About 40, 10 from perradial to perradial, hollow, long, with conical laterally compressed basal bulb, with abaxial spur and ocellus. No rudimentary marginal tentacles |
| Stomach | Large, pyramidal, almost filling upper ⅓ of subumbrellar cavity, attached about ⅘ of length to subumbrellar perradii | Large, with broad base, about half-height of subumbrellar cavity, attached to subumbrellar perradii for about ⅘ of its length | Large, filling completely subumbrellar cavity, attached ⅓ of its length to subumbrellar perradii |
| Mouth | 4 perradial lips with folded crenulate edges | 4 lips with folded crenulate margins | 4 perradial lips with complexly folded crenulate edges reaching border of umbrella |
| Gonads | On entire interradial walls of stomach, forming coarse meshwork of ridges and pits, surrounding the stomach | Very fine meshwork of pits, interradially on stomach, close-meshed irregular network of ridges with pits between them | Extended over interradial and perradial zones covering completely stomach, forming network of ridges and oval pits |

Table 1.—Continued.

| Characteristics | *Pandea conica* (Quoy & Gaimard, 1827) | *Pandea rubra* Bigelow, 1913 | *Pandea cybeles*, n. sp. |
|---|---|---|---|
| Color | Stomach and gonads reddish, brownish or yellowish. Mouth lips reddish or pink, tentacles milky yellow, ocelli red or reddish brown. Subumbrella colorless | Subumbrella, stomach, mouth, gonads and marginal tentacles deep brownish red or chocolate | Stomach, mouth, gonads and border of umbrella pink with light purple and violet tones |
| Distribution | Atlantic, Mediterranean | Bermuda, NW Pacific, Bering Sea, British Columbia. Probably inhabiting deep waters | Sargasso Sea |

*conica* and *Pandea cybeles* are more closely related, as both have a long conical process at the top of the umbrella. Therefore, a discussion on the descriptions of *Pandea conica* published by various authors will enlighten the separation of the species.

There is some disagreement among the various authors on the number of marginal tentacles, as well as in the proportion of height and width of the umbrella. It appears in some instances that authors were including under *Pandea conica* specimens belonging to different species.

However, all authors basically agree, when defining *Pandea conica,* that the height of the umbrella is about twice its width, the manubrium extends only along the upper ⅓ or half of the subumbrellar cavity, and the number of ribs on exumbrella and marginal tentacles is in the 20's, about 24.

A chronological review of descriptions by various authors follows.

Quoy & Gaimard (1827) first described the medusa as *Dianaea conica,* collected near the Strait of Gibraltar, as body elongated conically pointed at the top, "tentacles small, filamentous, in the 20's, with reddish spot at their base. The umbrella presented as many striae as tentacles. Manubrium with 4 small short arms, pink in color, the rest of the medusa transparent." Their illustration of the medusa shows size proportions of umbrella, stomach and tentacles.

Maas (1904) found abundant specimens of *Pandea conica* at Monaco Bay, and those had 8, 16, or 20 tentacles.

Mayer (1910) described *Pandea conica* as "barrel-shape sides bluntly pointed, 21 mm high and 10 mm wide, with 8 to 24 well developed longitudinal rib-like ridges along exumbrella and equal number of marginal tentacles with abaxial ectodermal ocelli. Stomach wide and short with 4 folded lips having sinuous margins." The colors of gonads, tentacles, and ocelli were brownish red, yellowish-milky and dark purple, respectively. Mayer's illustration (1910:117) shows short additional ridges extending up to ⅓ from the border of the umbrella, and the conical top is missing. Either this is an illustration of a newly-born medusa or it is not *P. conica*.

Vanhöffen (1911) indicated *P. conica* 12.5 mm high and 10 mm wide with conical process of 2 mm, 4 radial canals and ring canal. The largest specimens had 19 or 20 tentacles. Other characteristics agreed with descriptions by other authors.

Hartlaub (1913) also indicated the umbrella extending into a conical process at the top, being 21 mm high and 10 mm wide, with 24 marginal tentacles, and the stomach extending along the upper ⅓ of the subumbrellar cavity. Gonads and color agree with previous descriptions. Figure 286 on page 339 of Hartlaub 1913 illustrates his description.

Browne (1916) referred to *Pandea* juvenile specimens obtained at the Chagos Archipelago, which could be related to *Pandea conica*. The smallest was about 2.5 mm in diameter.

Uchida (1927) discussed the characteristics of *Pandea conica* and *P. rubra*. He identified and described specimens obtained at Misaki, Japan, as *Pandea conica*, with "bell somewhat prismatic, with truncated top, 30 mm high and 17 mm wide; exumbrella with 44 longitudinal ridges. 4 Radial canals, wide, jagged, widest in the lower half. Ring canal narrower. Tentacles 44, all of similar length, hollow. Manubrium wide and short, nearly filling the upper half of bell cavity, fused with the upper part of subumbrella." The rest of the descriptive part agrees with other authors, in gonads, color, etc. He explained, "Ocellus could not be found in preserved specimens."

The truncate top of the umbrella of Uchida's specimens indicates that those specimens apparently do not belong to *Pandea conica* (see fig. 38, page 214 of Uchida 1927).

Ranson (1936) discussed the characteristics of species of *Pandea*, mainly referring to *P. conica* and *P. rubra*. The collections Ranson analyzed included abundant specimens or various sizes, enabling him to determine series of development of the medusa. A table on page 83 compiles the characteristics of *P. conica* as described by various authors. Analysis of data in that table suggests that under *P. conica* were included some specimens belonging to other species.

Russell (1953) described *P. conica* with higher than wide umbrella, conical summit, 16 to 24 longitudinal exumbrellar nematocyst ribs and corresponding number of marginal tentacles; jelly fairly thick. Velum narrow. Stomach pyramidal filling upper half of subumbrellar cavity, etc.

Kramp (1961) described *P. conica* "up to 21 mm high, 10 mm wide, with a conical apex terminating with a peculiar patch of thickened ectoderm; exumbrella with longitudinal ribs and ridges. Manubrium about half as long as bell cavity, with short mouth tube and folded lips. Radial canals fairly narrow, smooth. 16–24 tentacles with laterally compressed basal bulbs, with abaxial ocellus."

Radial canals in *P. conica* as described by Kramp (1961) do not agree with those in *P. cybeles*, which are wide with jagged outlines.

According to Kramp (1961) the *Pandea conica* of Bigelow (1918) found between Chesapeake Bay and Bermuda is possibly a new species.

The main anatomical features used to distinguish species of *Pandea* are: shape, dimensions, and characteristics of umbrella; shape and dimensions of stomach; characteristics of canals; number and characteristics of tentacles.

In *Pandea conica* according to most authors, the height of the umbrella is almost twice its width. The stomach occupies the upper ⅓ or probably half of the subumbrellar cavity. Ribs and tentacles are in the 20's, usually up to 24.

In *Pandea cybeles*, width and height of umbrella are rather similar, only slightly higher than wide. The stomach is large, filling completely the subumbrellar cavity, extending to the edge of the umbrella. Ribs and marginal tentacles number 40.

Differences between *P. conica* and *P. cybeles* are clear when comparing the illustrations by Quoy & Gaimard (1827), Hartlaub (1913), Russell (1953), and Kramp (1959, 1965), with those of *P. cybeles* in the present work.

*Distribution.*—The medusa is a meroplanktonic stage. Specimens of *Pandea*, including *Pandea cybeles* have been mainly obtained far offshore at oceanic localities.

Therefore, the medusae experience wide oceanic distribution, enjoying a long-lived pelagic medusoid stage. Kramp (1959) stated that the large size of the medusae may indicate a long pelagic life, which is advantageous for increasing dispersion of the population, with the opportunity to be transported by currents to regions distant from the normal habitat of the species. Kramp (1959) also suggested that in *Pandea conica,* wide oceanic distribution is due to the fact that its hydroid is attached to the shell of the pteropod *Cleodora cuspidata.*

Segura (1984) found specimens of *Pandea* sp. at several locations northwest of the Galapagos Islands, off Ecuador and Peru. They were juvenile specimens of some species of *Pandea,* with umbrella 1.0 to 3.0 mm high and 1.0 to 2.0 mm wide, with no apical projection, umbrella of thick mesoglea, exumbrella with longitudinal rows of nematocyst tracks in same number as marginal tentacles. Velum narrow. Stomach large, filling almost completely the subumbrellar cavity. Radial canals wide, circular canal narrow. Marginal tentacles up to 24, tentacular basal bulbs conical, laterally compressed. No ocelli at basal bulb of tentacles.

*Pandea conica* has been observed near Bermuda (Bigelow 1918, 1938), China (Chiu 1954), Gibraltar (Hartlaub 1913), Tristan de Cunha (Haeckel 1879), Alboran Sea, Tirrhenian Sea, Sidra Sea, Messina, Aegean Sea, Marmora Sea, Strait of Gibraltar (Kramp 1924), Japan and Philippine Islands (Kramp 1928), Gulf of Guinea (Kramp 1955), West Africa and off Argentina (Kramp 1957), Sargasso Sea, west of Spain, east of Azores (Kramp 1959), East Africa, Ceylon, East Australia, New Zealand, Vietnam (Kramp 1968), Strait of Gibraltar (Quoy & Gaimard 1827), Mediterranean Sea (Ranson 1936), Japan (Uchida 1927), Agulhas Current (Vanhöffen 1911), China Seas (Zhang 1979).

*Pandea rubra* has been recorded from British Columbia and Puget Sound (Arai & Brinckmann-Voss 1980), Gulf of Alaska, Aleutians, Southeast Kamchatka, Sea of Okhotsk, San Francisco (Bigelow 1913), Bermuda (Bigelow 1938), West Ireland (Kramp 1920), west of British Isles (Kramp 1929, Russell 1953), south and southwest of Iceland (Kramp 1926), South Africa, Weddell Sea, Antarctic (Kramp 1957a, b), Northwest Pacific, Ceylon, Northeast Pacific (Kramp 1965), USSR Far East waters (Naumov 1956), Cochin, Malabar-Trivandrum coastal waters (Vannucci et al.1970).

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## Literature Cited

Arai, M. N., & A. Brinckmann-Voss. 1980. Hydromedusae of the British Columbia and Puget Sound.—Canadian Bulletin of Fisheries and Aquatic Sciences (204):1–192.

Bigelow, H. B. 1913. Medusae and Siphonophorae collected by the U.S. Fisheries Steamer ALBATROSS in the Northwestern Pacific 1906.—Proceedings of the U.S. National Museum 14: 1–119.

———. 1918. Some Medusae and Siphonophorae from the Western Atlantic.—Bulletin of the Museum of Comparative Zoology at Harvard College 63:365-442.

———. 1938. Plankton of the Bermuda Oceanographic Expeditions. VIII Medusae taken during the years 1929 and 1930.—Zoologica (New York) 23(5):99–189.

Browne, E. T. 1916. Medusae from the Indian Ocean. The Percy Sladen Trust Expedition.—Transactions of the Linnean Society of London (Zoology), series 2, 17:169–210.

Chiu, S. T. 1954. Studies on the Medusae fauna of the South-eastern China coast with notes on their geographical distribution.—Acta Zoologica Sinica 6(1):49–57.

Haeckel, E. 1879. Das System der Medusen. Erster Theil einer Monographie der Medusen. Pp. 1–360. Jena.

Hartlaub, V. 1913. Craspedote Medusen. Teil I, Lief. 3, Family Tiaridae.—Nordisches Plankton (17)12:237–363.

Kramp, P. L. 1920. Anthomedusae and Leptomedusae.—Report of the Scientific Research of the MICHAEL SARS North Atlantic Deep Sea Expedition 3(2):1–24.

———. 1924. Medusae.—Report on the Danish Oceanographic Expeditions 1908–1910 to the Mediterranean and Adjacent seas (8)2, Biol. K1: 1–40

———. 1926. Medusae II. Anthomedusae.—Danish Ingolf Expedition 5(10):1–102.

———.1928. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. XLIII Hydromedusae. I Anthomedusae.—Videnskabelige Meddelelser Dansk Naturhistorisk Forening i København 85: 27–64.

———. 1955. The Medusae of the tropical west coast of Africa.—Atlantide Report 3:239–324.

———. 1957a. Hydromedusae of the DISCOVERY Collections.—Discovery Reports 29:1–128.

———. 1957b. Medusae.—British-Australian-New Zealand Antarctic Research Expedition 1929–31, (B)6:151–164.

———. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters.—Dana Reports (46): 1–283.

———. 1961. Synopsis of the Medusae of the World.—Journal of the Marine Biological Association of the United Kingdom 40:1–469.

———. 1965. The Hydromedusae of the Pacific and Indian Oceans.—Dana Reports (63):1–162.

———. 1968. The Hydromedusae of the Pacific and Indian Oceans.—Dana Reports (72):1–200.

Maas, O. 1904. Méduses provenant des Campagnes des yachts HIRONDELLE et PRINCESS ALICE.—Résultats des Campagnes Scientifiques, Monaco 28:1–71.

Mayer, A. G. 1910. Medusae of the World.—Carnegie Institution of Washington Publication 109: 1–735.

Naumov, D. V. 1956. Medusae in the Far-eastern waters of the Soviet Union.—Akademia Nauk SSSR. Zoologicheskii Institut. Trudy Problemnykh i Tematisheskikh Soveshchsnii 6:34–41. [In Russian]

Quoy, J. R. C., & J. P. Gaimard. 1827. Observations zoologiques faites à bord de l'ASTROLABE, en mai 1826, dans le détroit de Gibraltar.—Annales des Sciences Naturelles, Paris 10:1–21, 172–193.

Ranson, G. 1936. Méduses provenant des Campagnes du Prince Albert I de Monaco.—Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert I, Prince Souverain de Monaco 92:1–245.

Russell, F. S. 1953. The Medusae of the Brtitish Isles. Cambridge University Press, p. 1–530.

Segura, L. 1984. Morfología, sistemática y zoogeografía de las medusas (Cnidaria, Hydrozoa, Scyphozoa) del Pacífico Tropical Oriental.—Publicación Especial del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM) 8:1–320.

Uchida, T. 1927. Studies on Japanese Hydromedusae. I. Anthomedusae.—Journal of the Faculty of Sciences Imperial University of Tokyo, Section 4, Zoology 1(3):145–241.

Vanhöffen, E. 1911. Die Anthomedusen und Leptomedusen des Deutschen Tiefsee Expedition 1898–1899.—Wissenschaften Ergebnisse VALDIVIA 19(5):191–233.

Vannucci M., V. Santhakumari, & E. P. dos Santos. 1970. The ecology of Hydromedusae from Cochin area.—Marine Biology 7:49–58.

Zhang, J. 1979. A preliminary analysis of the hydromedusae fauna of the China Sea areas.—Acta Oceanologica Sinica 1(1):127–237.

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# Rearing, development, and early life history of the California Needlefish, *Strongylura exilis*

by David A. AMBROSE * and H. Geoffrey MOSER *

## Abstract

Fertilized eggs were obtained from field-caught specimens of California needlefish, *Strongylura exilis*, and incubated in an experimental aquarium to obtain developmental series of embryos, larvae, and juveniles. The spherical eggs are 2.4-2.7 mm in diameter and have 28-40 elongate filaments evenly spaced over the shell. At hatching (10-19 days after fertilization) the larvae have functional eyes, jaws, digestive tracts and caudal fins and are covered with xanthic and melanistic pigment. Newly hatched larvae fed immediately on larvae of brine shrimp and grew rapidly ( 1 mm/day). Late larvae and early juveniles continued rapid growth on a diet of frozen adult brine shrimp and chopped squid. Allometric growth of the upper and lower jaws produces a "halfbeak" stage which reaches a maximum at 24 mm body length when the relative difference in "beak" length is 27 % of body length. During the developmental period the sheath of melanophores and xanthophores which covers the body changes to a zonal pattern consisting of a greenish black dorsum and two lateral silvery zones.

## Introduction

The California needlefish, *Strongylura exilis*, is the most common representative of the family Belonidae in the California Current region. It ranges from Peru to San Francisco (including the Galapagos Islands) usually inhabiting bays and harbors at or near the surface in small schools (**Fitch & Lavenberg** 1971; **Eschmeyer** et **al.** 1983). This excellent food fish can grow as large as 91 cm and is occasionally taken on hook and line by sport fishermen, but is not fished commercially.

Although eggs and larvae of other needlefish species have been described (**Ryder** 1882 ; **D'Ancona** 1931 ; **Mito** 1958 ; **Breder** 1959 ; **Masurekar** 1967 ; **Foster** 1973 ; **Rosenthal & Fonds** 1973 ; **Hardy** 1978) early life history information on *S. exilis* is scanty. In their review of beloniform ontogeny, **Collette** et **al.** (1984) illustrated the egg and an 8.6 mm larva of *S. exilis* and listed the egg diameter and filament arrangement in a summary table. The purpose of this paper is to describe the eggs, larvae, and juveniles of a complete developmental series of *S. exilis* reared in the experimental aquarium of the Southwest Fisheries Center, with special emphasis on the ontogenetic changes in color pattern.

## Methods and Materials

Five adult specimens of *S. exilis* were collected in a 24 m beach seine over sandy substrate north of Scripps Institution of Oceanography (SIO) pier on June 13, 1979. The two males (435 and 480 mm SL) and three females (500-636 mm SL) were mature and free-running eggs from the largest female were artificially fertilized at 0830 hrs. with sperm from macerated testes of the largest male. The five specimens were preserved and deposited in the SIO fish collection (cat. no. 79-88).

The fertilized eggs were taken to the Southwest Fisheries Center experimental aquarium for incubation. The incubation container was a white plastic cylinder (diameter = 28 cm, depth = 8 cm) with a 500 $\mu$m nylon mesh bottom. This was partially immersed in a 100 l cylindrical black fiberglass container that was placed in a large water bath. The eggs were bathed in a constant stream of sea water which ranged from 19° to 21 °C during the incubation period. After hatching the larvae were placed in a 100 l rearing container in the water bath. Sea water volume in the rearing container was maintained at about 80 l and a liter of dense algal culture (*Tetraselmis suesica* or *Dunaliella* sp.) was added every few days to maintain water quality. Since the rearing container was non-circulating, gentle aeration was used to prevent stratification. The tanks were illuminated by four 40 watt fluorescent lamps about 1 m from the surface on a 12 hour day/12 hour night cycle.

After hatching, the larvae were fed nauplii of brine shrimp (*Artemia* sp.) daily at a minimum concentration of one nauplius/ml. Late stage larvae and juveniles were fed frozen brine shrimp, chopped squid, and occasionally larvae of the queenfish, *Seriphus politus*. Eggs and larvae were regularly sampled and preserved in 4 % formalin. Some were photographed before preservation to record xanthic pigmentation.

The sequence and timing of egg developmental events was described using stages formulated by Oppenheimer (1937). A developmental series of larvae and juveniles was established to study ontogenetic changes in morphology, morphometrics and pigmentation. Subsequently, selected specimens from this series were stained with Alizarin Red-S and cleared in a graded series of KOH and glycerin to determine the sequence of formation of ossified fin rays. For larger specimens, X-radiographs were also used to determine fin ray development.

Because of allometric growth of the snout during development the anterior margin of the eye, rather than the anterior tip of the snout was used as the reference point in making longitudinal morphometric measurements. Thus, for morphometric comparisons, body length (BL) is defined as the distance from the anterior margin of the eye to the posterior margin of the hypural plate. Snout length and lower jaw length are measured from the tip of each jaw to the anterior margin of the eye. Head length is measured from the anterior margin of the eye to the cleithrum and the anterior margin of the eye is the anterior reference point for measurements to the anus and fin origins. Standard length (SL) is the distance from the tip of the upper jaw to the posterior margin of the hypural plate. All other measurements follow the definitions of **Ahlstrom** et **al.** (1976).

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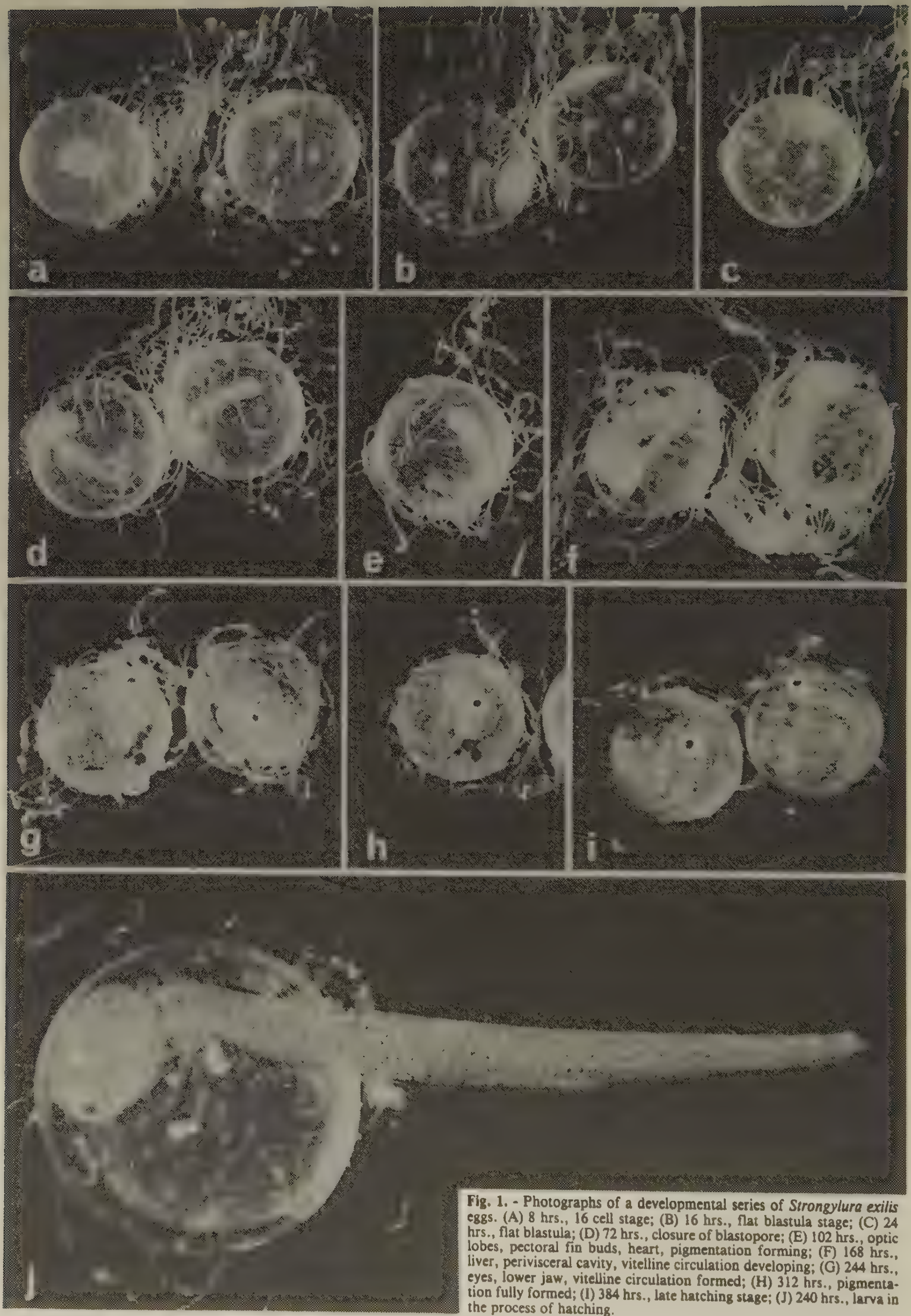

**Fig. 1.** - Photographs of a developmental series of *Strongylura exilis* eggs. (A) 8 hrs., 16 cell stage; (B) 16 hrs., flat blastula stage; (C) 24 hrs., flat blastula; (D) 72 hrs., closure of blastopore; (E) 102 hrs., optic lobes, pectoral fin buds, heart, pigmentation forming; (F) 168 hrs., liver, perivisceral cavity, vitelline circulation developing; (G) 244 hrs., eyes, lower jaw, vitelline circulation formed; (H) 312 hrs., pigmentation fully formed; (I) 384 hrs., late hatching stage; (J) 240 hrs., larva in the process of hatching.

Développement des oeufs de *Strongylura exilis*, de 8 à 384 heures.

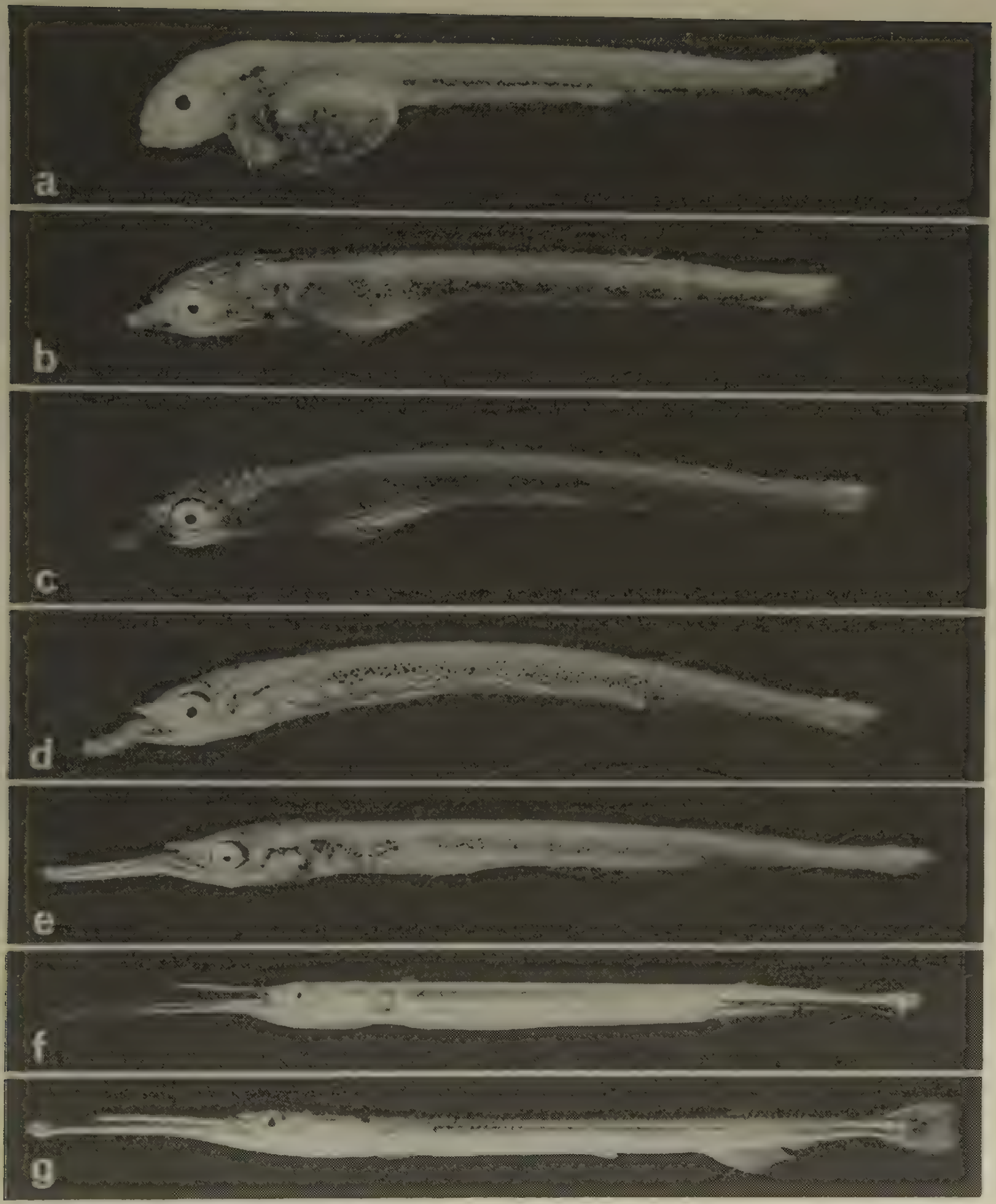

Fig. 2. - Photographs of developmental series of *Strongylura exilis.* (A) 9.1 mm BL, new hatched; (B) 9.6 mm BL, day 1; (C) 10.6 mm BL, day 2; (D) 12.6 mm BL, day 3; (E) 16.5 mm BL, day 6; (F) 32.5 mm BL, day 18; (G) 44.4 mm BL, day 28.

Développement de *Strongylura exilis,* de l'éclosion à 28 jours.

Table 1
Developmental features of *Strongylura exilis* eggs

| Hours after fertilization | Stage (Oppenheimer 1937) | Developmental features |
|---|---|---|
| 2-1/4 | 2 | Fertilized |
| 4 | 3- 4 | 2 and 4 cell stages |
| 8 | 5- 6 | 16-cell stage |
| 12-1/2 | 8- 9 | Early to late high blastula |
| 16 | 10 | Flat blastula |
| 20 | 10 | Flat blastula |
| 24 | 10-11 | Flat blastula and expanding blastula |
| 32 | 12 | Early gastrula |
| 49-1/2 | 13-14 | Mid to late gastrula |
| 72 | 15-17 | Closure of blastopore; embryo, central nervous systems, optic vesicles, somites forming |
| 102 | 20-22 | Midbrain expanded to form optic lobes; heart forming and beating; pectoral fin bud forming; pigment forming on yolk and embryo |
| 120 | 23-24 | Xanthophores and melanophores scattered over yolk and beginning to cover embryo; embryo showing axial flexion |
| 145 | 25 | Formation of urinary vesicle |
| 168 | 27-28 | Liver and perivisceral cavity forming; pectoral fin buds rounded; xanthic pigment solid over embryo, except over dorsal midline and less concentrated over brain; perivisceral walls becoming pigmented |
| 193-1/2 | 29 | Notochord flexion; pectoral fins beating and fish flipping; xanthic and melanistic pigment over entire head and body |
| 222-1/2 | 30 | Lower jaw forming |
| 244 | 31 | Fin rays in caudal fin; lower jaw formed; jaws, eyes, and body moving |
| day 10-19 | 32 | Hatching |

## Description of Development

### Eggs

*S. exilis* eggs are among the smallest known for Belonidae. The diameter for 25 measured eggs was 2.44-2.72 mm ($\bar{x}$ = 2.57 ± 0.061 SD). Each spherical egg has 28-40 ($\bar{x}$ = 33.3 ± 3.06 SD for 25 eggs) evenly spaced filaments singly attached to the thick chorion by a swollen truncated cone. The filament lengths of 13.5 > 26.7 mm are among the largest reported from this family. These filaments are intertwined with those of adjacent eggs forming adhesive clumped egg masses which attach to vegetation or floating objects. The clear yolk is unsegmented and oil globules are absent.

Developmental features of the egg of *S. exilis* conform closely to the stages of egg development of *Fundulus heteroclitus* described by Oppenheimer (1937). Using these criteria, the timing of developmental events in *S. exilis* eggs is summarized in Table 1. Early cleavage stages are completed within 12 hours after fertilization (fig. 1A, B). The blastula undergoes epiboly at about 24 hours, marking the beginning of gastrulation (fig. 1C). By 72 hours after fertilization the blastopore has closed and the embryo is well established, with a central nervous system, optic vesicles, and somites forming (fig. 1D). At 102 hours the heart is beating and xanthic (yellow) and melanistic (black) pigment is forming on the embryo and yolk (fig. 1E). At 168 hours the embryo is advanced, has well developed eyes, brain lobes and pectoral fins. Xanthic pigment covers the entire embryo except the mid-dorsal line and is scattered evenly over the yolk. Melanophores also cover the embryo except for the region over the medulla and the dorsal midline of the body. They are concentrated over the developing perivisceral region at the sides of the body and over the vitelline circulatory vessels on the surface of the yolk (fig. 1F). By 193-1/2 hours, the developing fish is flipping its tail, the pectoral fins are beating, and the tip of the notochord is flexing. At 244 hours the eyes are fully formed, the caudal fin rays and median finfold are developing and the jaws and digestive tract are formed. The eyes are silvery and the head and body are covered with xanthophores and melanophores. Xanthophores are distributed sparsely over the yolk and melanophores remain concentrated along the vitelline vessels. The pectoral and caudal fins and the median finfold lack pigment (fig. 1G).

Hatching (fig. 1J) began at 244 hours (day 10) and most of the eggs had hatched by day 16, however, a few eggs remained unhatched until day 19.

### Larvae

**General morphology**: The yolksac of newly hatched larvae is oblate in shape and ranges in length from 2.0 to 2.5 mm, in height from 1.2 to 1.7 mm, and in volume from 2.77 to 5.56 cu. mm. Yolk sac dimensions for a larva 1 day after hatching were 1.9 x 1.1 mm with a volume of 2.08 cu. mm and a larva 2 days old had a yolk sac 0.65 x 0.50 mm with a volume of 0.89 cu. mm. By day 3 the yolk sac is resorbed (fig. 2). Length of the larvae at hatching ranges from 6.1 mm to 9.1 mm BL.

Larvae are well differentiated at hatching with functional eyes, jaws and digestive tract (fig. 2A). The most pronounced morphological change during development is the increase in length of the snout and lower jaw (table 2; fig. 2). At hatching the mouth is slightly subterminal to subequal. The lower jaw grows rapidly, attaining a length 33 to 41 % of the body length in specimens 23.8 to 54.8 mm BL and 42 to 47 % of the body length for the 55.1 to 111.0 mm BL size range. The upper jaw grows more slowly and is about 1/2 the length of the lower jaw at 32.0 mm BL (fig. 2F). Thereafter growth is rapid, with upper jaw length reaching 88 to 92 % of lower jaw length in specimens ranging from 68.5 mm to 111.0 mm BL. Allometric growth of the upper and lower jaws produces a "halfbeak" stage which reaches a maximum at about 24 mm BL when the relative difference in "beak" length reaches 27 % of BL.

Table 2
Measurements (mm) of early stages of *Strongylura exilis*

| Body length | Age (days) | Standard length | Snout length | Lower jaw length | Head length | Eye to anus distance | Eye to anal fin origin | Eye to dorsal fin origin | Eye to pelvic fin origin | Pelvic fin length | Body depth | Pectoral fin length | Pectoral fin depth | Eye width | Eye height |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6.2 | 0 | 6.3 | 0.1 | 0 | 0.9 | 4.2 | – | – | – | – | 0.4 | 0.4 | 0.4 | 0.5 | 0.4 |
| 6.8 | 0 | 7.0 | 0.2 | 0.08 | 1.1 | 4.7 | – | – | – | – | 0.6 | 0.6 | 0.4 | 0.5 | 0.4 |
| 8.2 | 0 | 8.4 | 0.2 | 0.2 | 1.3 | 5.6 | – | – | – | – | 0.7 | 0.7 | 0.4 | 0.6 | 0.5 |
| 9.9 | 1 | 10.2 | 0.3 | 0.7 | 1.5 | 6.8 | 7.2 | 7.7 | – | – | 1.4 | 0.8 | 0.4 | 0.6 | 0.6 |
| 10.2 | 2 | 10.6 | 0.4 | 0.9 | 1.6 | 7.3 | 7.5 | 8.0 | – | – | 1.2 | 1.0 | 0.5 | 0.7 | 0.6 |
| 12.3 | 3 | 13.0 | 0.7 | 1.8 | 1.9 | 8.6 | 8.7 | 9.7 | – | – | 1.3 | 0.9 | 0.5 | 0.8 | 0.6 |
| 13.4 | 4 | 14.2 | 0.8 | 2.4 | 2.0 | 9.7 | 9.8 | 10.4 | – | – | 1.4 | 1.1 | 0.6 | 0.8 | 0.7 |
| 16.2 | 6 | 17.2 | 1.0 | 3.8 | 2.3 | 11.0 | 11.2 | 11.8 | – | – | 1.4 | 1.4 | 0.6 | 0.9 | 0.7 |
| 17.5 | 8 | 18.8 | 1.2 | 4.8 | 2.6 | 12.0 | 12.2 | 12.8 | – | – | 1.6 | 1.5 | 0.7 | 1.0 | 0.8 |
| 23.0 | 10 | 25,4 | 2.4 | 5.4 | 3.6 | 16.2 | 16.5 | 17.0 | 12.3 | 0.5 | 1.9 | 2.1 | 0.8 | 1.2 | 1.1 |
| 23.8 | 10 | 26.1 | 2.2 | 8.6 | 3.6 | 16.2 | 16.7 | 17.7 | 12.0 | 0.5 | 2.0 | 1.9 | 0.8 | 1.2 | 1.1 |
| 27.0 | 12 | 29.9 | 2.9 | 9.2 | 3.9 | 18.4 | 18.7 | 19.7 | 14.2 | 0.5 | 1.9 | 2.3 | 0.8 | 1.3 | 1.1 |
| 32.0 | 17 | 38.4 | 6.4 | 13.0 | 5.0 | 21.8 | 22.2 | 23.4 | 16.8 | 0.9 | 2.4 | 2.5 | 1.0 | 1.7 | 1.5 |
| 32.5 | 18 | 38.5 | 6.0 | 12.3 | 5.0 | 22.5 | 22.9 | 24.0 | 17.2 | 0.8 | 2.3 | 2.8 | 1.2 | 1.5 | 1.4 |
| 48.8 | 39 | 63.1 | 14.3 | 17.3 | 7.9 | 32.8 | 33.0 | 36.5 | 24.0 | 2.3 | 2.8 | 4.6 | 1.5 | 2.7 | 2.2 |
| 50.7 | 39 | 65.2 | 14.5 | 19.0 | 8.3 | 35.1 | 35.9 | 38.1 | 27.0 | 2.1* | 2.7 | 4.6* | 1.4 | 2.7 | 2.3 |
| 54.8 | 35 | 70.5 | 15.7 | 18.0 | 8.9 | 37.9 | 38.6 | 40.4 | 28.9 | 2.6* | 3.6 | 5.2 | 1.5 | 2.8 | 2.5 |
| 55.1 | 39 | 73.6 | 18.5 | 23.3 | 9.6 | 38.3 | 39.0 | 41.3 | 29.0 | 2.4 | 3.2 | 5.2 | 1.6 | 2.8 | 2.2 |
| 55.8 | 36 | 72.3 | 17.1 | 24.6 | 9.2 | 39.3 | 40.2 | 42.5 | 29.6 | 2.6 | 3.8 | 5.1 | 1.7 | 2.7 | 2.3 |
| 58.1 | 44 | 79.1 | 21.0 | 26.7 | 9.8 | 39.3 | 39.6 | 41.8 | 30.1 | 2.6* | 3.8 | 5.2 | 1.6 | 2.9 | 2.8 |
| 68.5 | 57 | 87.3 | 18.8* | 20.6 | 11.2 | 47.4 | 48.2 | 50.4 | 36.6 | 2.9* | 4.1 | 6.2 | 1.7 | 3.5 | 3.2 |
| 79.2 | 73 | 109.3 | 30.1 | 34.1 | 11.7 | 54.0 | 55.0 | 56.7 | 40.3 | 3.5 | 5.7 | 7.7 | 2.3 | 4.0 | 3.8 |
| 79.9 | 96 | 113.5 | 33.6 | 37.8 | 13.8 | 56.2 | 57.4 | 60.2 | 43.4 | 4.2 | 6.1 | 8.6 | 2.1 | 4.2 | 3.9 |
| 80.0 | 81 | 112.7 | 32.7 | 35.9 | 12.8 | 56.1 | 57.1 | 59.3 | 43.1 | 4.0 | 5.5 | 8.0 | 2.2 | 4.2 | 3.8 |
| 111.0 | 120 | 155.8 | 44.8 | 48.6 | 17.0 | 75.3 | 77.0 | 81.0 | 57.6 | 5.5 | 7.7 | 11.7 | 3.3 | 5.7 | 5.7 |

* Indicates damaged fin or other structure.

Teeth begin to form on the lateral margins of the lower and upper jaws at day 2. Tooth development increases rapidly and by day 10 a pattern of widely spaced dagger-like teeth with smaller closely spaced teeth between them is apparent. Initially, teeth are formed on the lower jaw somewhat anterior to the tip of the upper jaw but by about day 18 (32.5 mm BL) teeth are forming simultaneously as the jaws elongate. The upper jaw is narrower than the lower jaw and, when closed, fits into a groove in the latter. Only the fleshy tip of the lower jaw lacks teeth in our largest specimens.

In contrast to the allometry of jaw growth most other body proportions remained remarkably constant through the growth series. This is shown by the mean values and standard deviations for proportions measured over the entire growth series: (1) head length/BL = 15.7 % ± 0.88, (2) eye to anus/BL = 69 % ± 1.37, (3) eye to anal fin origin/BL = 70.5 % ± 1.50, (4) eye to dorsal fin origin/BL = 74.6 % ± 1.99, and (5) body depth/BL = 7.9 % ± 2.02. Eye width is initially about 1/2 the head length and undergoes a relative decrease to about 1/3 the head length in specimens larger than 23.0 mm BL. At hatching eye height is about 75 % of eye width and undergoes a relative increase throughout the developmental period until the eye becomes round in our largest specimens.

**Fin development/meristics**: Notochord flexion and the initial ossification of the principal caudal rays occurs approximately 2 days before hatching; however, the full complements of 7 + 8 principal and 6 + 6 procurrent rays are not ossifying until about 11.3 mm and 32.5 mm BL, respectively (table 3). Dorsal, anal, and pectoral fin ray elements and the vertebral centra are ossifying during the first

Table 3
Meristics of larvae and early juveniles of *Strongylura exilis*

| Body length | Age (days) | Vertebrae | Caudal fin rays: Principal | Caudal fin rays: Procurrent | Dorsal fin rays | Anal fin rays | Pectoral fin rays | Pelvic fin rays |
|---|---|---|---|---|---|---|---|---|
| 6.4 | unhatched | – | 1 + 2 | 0 + 0 | – | – | – | – |
| 6.7 | " | – | 1 + 2 | 0 + 0 | – | – | – | – |
| 8.3 | 0 | 42 | 4 + 5 | 0 + 0 | X | 5 | 1 | – |
| 11.3 | 3 | 70 | 7 + 8 | 0 + 0 | 15 | 16 | 3 | – |
| 13.4 | 4 | 69 | 7 + 8 | 1 + 1 | 15 | 17 | 5 | – |
| 16.2 | 6 | 69 | 7 + 8 | 2 + 2 | 14 | 18 | 8 | – |
| 17.5 | 8 | 69 | 7 + 8 | 3 + 3 | 15 | 18 | 8 | – |
| 23.8 | 10 | 69 | 7 + 8 | 4 + 4 | 16 | 18 | 11 | – |
| 27.0 | 12 | 69 | 7 + 8 | 4 + 4 | 14 | 18 | 12 | X |
| 32.0 | 17 | 69 | 7 + 8 | 5 + 6 | 15 | 18 | 12 | 5 |
| 32.5 | 18 | 68 | 7 + 8 | 6 + 6 | 16 | 18 | 13 | 5 |
| 80.5 | 49 | 69 | 7 + 8 | 6 + 6 | 16 | 18 | 12 | 6 |

X = présent
– = absent

day after hatching. Full fin ray complements for dorsal (12-16) and anal (15-20) are ossifying by 11.3 mm BL (3 days after hatching). The entire vertebral column (68-74 centra) is ossifying by 13.4 mm BL (day 4). The paired fin ray elements ossify later. Full pectoral fin ray complements (12-13) are formed by 27.0 mm BL (12 days after hatching). Pelvic fins are last to achieve the full complement of 6 rays usually between 32.5 mm (day 18) and 48.8 mm BL (day 39). The pelvic fins develop later in *S. exilis* than in any other known belonid species.

A prominent median finfold is present at hatching. The dorsal and anal finfolds begin at the level of the anus and join posteriorly with the caudal finfold. A pre-anal finfold is present between the yolk sac and the anus. The dorsal, anal, and caudal finfolds are lost as the rays develop, however, the pre-anal finfold persists until about 30 mm BL.

**Pigmentation**: At hatching the larva is covered with a sheath of melanophores and xanthophores. Both surfaces of the pectoral fin base are covered and the body sheath fans out onto the caudal fin rays. Areas which lack pigment are the branchiostegal membrane, the pectoral fin blades, the median finfold, and the terminus of the gut (fig. 2A). An internal melanistic streak lies above the gut and extends anteriad into the head beneath the otic region. Posterior to the gut the streak continues as heavy melanistic lines on each side of the anal fin. In hatchlings with large yolk sacs the melanophores are concentrated along the vitelline blood vessels and the xanthophores are scattered over the yolk sac. As the yolk sac decreases the melanophores and xanthophores gradually cover the entire region (fig. 2B, C).

At about day 3 guanine begins to form on the opercle and in the lining of the perivisceral cavity and these regions develop an aquamarine color that persists throughout the growth series (fig. 2D). By day 12 (27 mm BL) the melanistic pigment begins to diminish on the trunk region above the gut and this region develops a shiny guanine layer. The dorsum and upper trunk retains the melanistic and xanthic covering and by day 17 (32 mm BL) three distinct pigment zones are apparent on the trunk: (1) a dorsal zone extending about a third of the way down the trunk consisting of heavy melanistic pigment infused with residual xanthic pigment that is beginning to be replaced by bright green pigment, (2) a middle silvery zone with some melanophores, and (3) a ventral silvery aquamarine zone (fig. 2F). These zones continue posteriorly and converge towards the caudal fin. By day 28 (44 mm BL) the dorsal zone is bright green with a black background and yellow pigment is absent (fig. 2G). With continued development the lateral silvery zone widens and in our largest specimens (120 days; 110 mm BL) the dorsal zone is about 1/4 of the body depth and is entirely black.

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## References

**Ahlstrom (E.H.), J.L. Butler** and **B.Y. Sumida**, 1976. - Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distribution, and early life histories and observations on five of these from the northwest Atlantic. *Bull. Mar. Sci.* **26**: 285-402.

**Breder (C.M.Jr.)**, 1959. - Observations on the spawning behavior and egg development of *Strongylura notata* (Poey). *Zoologica*, **44** (10): 141-147.

**Collette (B.B.), G.E. McGowen, N.V. Parin** and **S. Mito**, 1983. - Beloniformes: Development and relationships, p. 335-354. *In*: **H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, Jr.** and **S.L. Richardson** (eds.), Ontogeny and systematics of fishes. *Spec. Publ. No.1, Amer. Soc. Ichthyol. Herpetol.*

**D'Ancona (U.)**, 1931. - Synentognathi: *in*: Uova, larvae e stadi giovanili di Teleostei. *Fauna Flora Golfo Napoli Monogr.* **38**: 157-161.

**Eschmeyer (W.N.), E. Herald** and **H. Hammann**, 1983. - A field guide to Pacific coast fishes of North America. *Peterson Field Guide Series* 28, Houghton Mifflin Co., Boston.

**Foster (N.R.)**, 1973. - Behavior, development, and early life history of the Asian needlefish, *Xenentodon cancila. Proc. Acad. Natur. Sci. Phila.* **125** (5): 77-88.

**Hardy (J.D.)**, 1978. - Development of fishes of the mid-Atlantic bight. An atlas of egg, larval, and juvenile stages. Vol. II. Anguillidae through Syngnathidae. *U.S. Fish Wildl. Serv. Biol. Serv. Program.* FWS/OBS-78/12.

**Masurekar (V.B.)**, 1967. - Eggs and developmental stages of *Tylosurus crocodilus* (Lesueur). *J. Mar. Biol. Ass. India*, **9** (1): 70-76.

**Miller (D.J.)** and **R.N. Lea**, 1972. - Guide to the coastal marine fishes of California. *Calif. Dep. Fish Game Bull.* 157.

**Mito (S.)**, 1958. - Eggs and larvae of *Tylosaurus melanotus* (Bleeker) Belonidae, p. 22. *In*: Uchida et al. (eds.), Studies on the eggs, larvae and juveniles of Japanese fishes. Ser. 1. *Fac. Agric. Kyushu Univ.* Fukuoka, Japan. (In Japanese).

**Oppenheimer (J.M.)**, 1937. - The normal stages of *Fundulus heteroclitus. Anat. Rec.* **68** (1): 1-15.

**Rosenthal (H.)** and **M. Fonds**, 1973. - Biological observations during rearing experiments with the garfish *Belone belone. Mar. Biol.* **21**: 203-218.

**Ryder (J.A.)**, 1882. - Development of the silver gar (*Belone longirostris*) with observations of the genesis of the blood in embryo fishes, and a comparison of fish ova with those of other vertebrates. *U.S. Fish. Comm. Bull.* **1** (1881): 283-301.

## RÉSUMÉ

### Elevage, développement et premiers stades du Poisson-aiguille californien *Strongylura exilis*

*Strongylura exilis* est le Bélonidé le plus commun en Californie. On le trouve d'ordinaire en petits bancs dans les eaux superficielles des criques et des ports. C'est un excellent Poisson de consommation, pouvant atteindre 91 cm, mais dont la pêche n'est pas commercialisée. Les documents sur les premiers stades de cette espèce sont rares et le présent travail se propose de décrire les œufs, les larves et les juvéniles obtenus par élevage dans un aquarium expérimental du *Southwest Fisheries Center*. Les géniteurs ont été pris dans la nature, mais l'insémination a été pratiquée artificiellement. Les œufs, sphériques, sont parmi les plus petits de la famille (2,4-2,7 mm) et ont 28 à 40 longs filaments régulièrement disposés sur leur coque. A l'éclosion, 10 à 19 jours après la fécondation à 19-20 °C, les larves sont nourries immédiatement de nauplies d'Artémias et leur croissance sera rapide (1 mm/jour) ; les yeux, les mâchoires, le tractus digestif et la nageoire caudale sont fonctionnels dès la naissance, et le corps est revêtu d'une couche de mélanophores et de xanthophores. Les derniers stades larvaires et les juvéniles poursuivent leur croissance rapide avec un régime d'Artémias adultes congelées et de Calmars hachés. La croissance allométrique des mâchoires la mandibule s'allongeant plus rapidement que la mâchoire supérieure aboutit à un stade "demi-bec" qui atteint un maximum lorsque la longueur du corps est de 24 mm et que la différence de longueur entre les deux mâchoires est égale à 27 % de la longueur du corps.

Au cours du développement, la couverture uniforme de chromatophores (mélanophores et xanthophores) évolue vers un patron rayé en long, comportant une région dorsale noire-verdâtre et des flancs argentés.

# Polar Bear *Ursus maritimus*

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Lentfer, Jack W., editor. 1988. *Selected Marine Mammals of Alaska: Species Accounts with Research and Management Recommendations.* Marine Mammal Commission, Washington, D.C.

Photograph by Steven C. Amstrup

# Polar Bear *Ursus maritimus*

Photograph by Steven C. Amstrup

Polar bears (*Ursus maritimus*) are long-lived, late-maturing carnivores that have relatively low rates of reproduction and natural mortality. Their populations are susceptible to disturbance from human activities, such as the exploration and development of mineral resources or hunting. Polar bear populations have been an important renewable resource available to coastal communities throughout the Arctic for thousands of years.

## BIOLOGY, LIFE HISTORY, AND HABITAT REQUIREMENTS

### Distribution and Movements

Polar bears inhabit most ice-covered seas of the Northern Hemisphere. They are circumpolar in distribution and have been reported as far north as 88°N latitude (Stefansson 1921, Papanin 1939). They occur as far south in the eastern Bering Sea as St. Matthew Island and the Pribilof Islands (Ray 1971), and are commonly found within 300 km of the Alaskan coast of the Chukchi and Beaufort seas, from Bering Strait to the United States–Canada border (Frame 1969; Amstrup, unpubl. data). Polar bears in the Chukchi Sea make extensive north–south migrations in relation to the position of the southern edge of the pack ice.

In winter and spring polar bears are commonly found in three distinct types of ice: shorefast ice with deep snow drifts along pressure ridges, the floe edge, and areas of moving ice with 7/8 or more ice cover (Stirling *et al.* 1981). In the western Canadian Arctic, subadult females and adult females with young cubs generally prefer shorefast ice, possibly because of the absence of large adult males in this type of habitat. Other classes of bears seem to prefer the floe edge and moving ice; 87% of all bear sightings in spring in the western Canadian Arctic were made on the floe edge and moving ice (Stirling *et al.* 1975). Lentfer *et al.* (1980) indicated that the pattern of distribution in the western Canadian Arctic may not apply off the coast of Alaska, where mature males tend to range far offshore in the early spring and move toward the coast as the breeding season progresses. Off the coast of Alaska, Lentfer (unpubl. data) and Amstrup (unpubl. data) found numerous subadults and females with young cubs in drifting ice and along the floe edge and suggested that neither of these two components of the Alaskan population prefers shorefast ice during the spring.

When ice forms in the fall, polar bears that have spent the summer on drifting ice north of Alaska move to the south. By late fall they are distributed seaward of the Beaufort and Chukchi seacoasts, and normally occur during the winter as far south as Bering Strait. In some years the bears range south of St. Lawrence Island. Polar bears are more abundant along the Alaskan coast in years when winds bring old ice near shore. As the ice breaks up and recedes north in spring and early summer, the bears move north. They remain on the drifting pack ice through the summer. Little is known of their distribution on the pack ice in Alaska during the summer (Lentfer 1972).

Lentfer (1974*a*) hypothesized that Alaska has two relatively discrete polar bear populations. He proposed that a line extending northwest from Point Lay, Alaska, separates the western and northern populations in Alaska. Ocean currents and movements of the ice may be partly responsible for this apparent separation (Lentfer 1971*a*). Bears in the northern population remain west of Banks Island, Canada, and east of a point near Point Barrow which has yet to be defined (Amstrup, unpubl. data).

Information concerning the concentration of mercury residue in liver and muscle tissues from bears captured in the western and northern areas supports the hypothesis that polar bears in Alaska are not a single, homogeneous population (Lentfer 1987). In addition, the studies by Manning (1971), Lentfer (1974*a*), and Wilson (1976) on skull and body size of polar bears in Alaska support this interpretation. However, this interpretation was not supported by information on the incidence and severity of *Trichinella* larva infestation in polar bear masseter muscle, which do not vary geographically in Alaska (Lentfer 1976*a*).

There are no physical barriers to prevent polar bears from moving across international boundaries. However, information from mark-recapture studies indicates that polar bears tend to be recaptured in the general area where they were originally marked. Mark-recapture studies indicate that animals move between Alaska and the mainland coast of western Canada, but not between Alaska and the rest of Canada, Greenland, and Svalbard (Lentfer 1974*a*, 1983; Stirling *et al.* 1975, 1981; Amstrup *et al.* 1986). At least three instances of movements between Alaska and the U.S.S.R. have been reported (Lentfer 1983). At present there is insufficient information to determine the significance of such movements.

Stirling *et al.* (1977*a*) reported that the only recovery of a significant number of bears in Alaska that had been marked in Canada followed unusual weather conditions in the springs of 1974 and 1975, when ice conditions were such that the numbers of ringed seals and bearded seals in the Beaufort Sea were severely reduced. Lentfer (1983) reported that bears marked in Alaska were recovered in Canada in 1973 and 1976, but not in 1974 and 1975. Population estimates for polar bears in the Beaufort Sea were found to be significantly lower between March 1974 and March 1975 than in the previous or subsequent 3 years (DeMaster *et al.* 1980). DeMaster *et al.* suggested that the change in numbers of bears was related to relative abundance of ringed seals and bearded seals. These data suggest that the distribution and abundance of polar bears in the Beaufort Sea are influenced by the number and availability of seals.

Recent radio-tracking studies indicate considerably more movement of animals within the Beaufort Sea than did previous studies (Amstrup 1986). Polar bears radio-tagged off the coast of Alaska between Point Barrow and Barter Island were later located as far east in the Canadian Beaufort Sea as Cape Bathurst, Northwest Territories. Movements of radio-tagged bears also occurred in the opposite direction, from the Canadian Beaufort to Point Barrow. The explanation for the apparent difference in the results of mark-recapture studies and radio-tracking studies is most likely related to the ability to follow a bear's movements between seasons as opposed to obtaining data mainly in the spring of each year.

In summary, the available evidence indicates that polar bears off the coast of Alaska are not part of a single, well-mixed population. Polar bears between the vicinity of Point Barrow and Cape Bathurst seem to constitute a single management unit. Polar bears found west of Point Barrow constitute at least one additional management unit. Some movements, documented by tag returns and radio-tracking, have been reported between the western Beaufort Sea and the Chukchi Sea, and between the U.S.S.R. and Alaska. However, such movements appear to be the exception rather than the rule. Amstrup (unpubl. data) hypothesized that atypical movement of Beaufort Sea bears to points west of Point Barrow during the winter of 1985–86 was related to ice conditions and prevailing currents that carried bears west of their former ranges.

### Population Size

Sound estimates of the abundance of polar bears in Alaska or trends in population levels currently do not exist. This is related to a number of factors. As stated previously, the degree to which local populations are discrete is not fully understood. In addition, the probability of sighting a bear is related to habitat type, and even under ideal sighting conditions many bears are not seen (Stirling *et al.* 1975). For example, it is much easier to detect a bear along the floe edge than in heavily ridged pack ice. At present there is no way *a priori* to stratify a survey to account for differences in ice type in different areas. Finally, the density of polar bears is low enough that logistic constraints generally preclude surveying at a level of effort that will provide meaningful population estimates or indices of abundance (see Eberhardt 1978).

In spite of these difficulties, progress has been made in estimating abundance or population trends. Initial efforts involved strip surveys with fixed-wing aircraft. Tovey and Scott (1957) reported that trophy hunters in 1956 and 1957 sighted 255 bears while searching 26,515 km$^2$, or an average sighting rate of 1 bear per 104 km$^2$. Searches were conducted from the villages of Point Hope, Wales, Lisburne, and Point Barrow. Working from a slightly larger data base for 1956–58, Scott *et al.* (1959) reported that polar bear trophy hunters saw 1 bear per 138 km$^2$. These density estimates were based on an average aircraft speed of 167 km/hour and a 0.40-km strip width. From 1959 through 1969, airborne hunters saw 1 bear per 147 km$^2$ (Amstrup *et al.* 1986) during flights similar in pattern to those reported by Tovey and Scott (1957). Amstrup *et al.* (1986) recognized that many bears were probably missed and that coverage was not random.

From a density of 1 bear per 104 km$^2$ and available habitat along the Alaskan coastline of 208,000 km$^2$, Tovey and Scott (1957) estimated that there were roughly 2,000 polar bears in Alaska. The estimate of available habitat was based on the average distance from the coastline (121 km) of bear sightings by hunting guides in aircraft. Radiotelemetry studies by Amstrup (1986) indicate that polar bears occupy a strip 280 km wide along the coast of Alaska; using this figure and an average density of 1 bear per 104 km$^2$ results in a total population estimate of 4,600 animals. Amstrup's estimate of the average width of area used by polar bears off the coast of Alaska is likely to be low, because it is based primarily on the distribution of females in the Beaufort Sea. Lentfer (pers. commun.) reported finding a significant number of polar bears in the Chukchi Sea beyond 280 km from the coast.

During 3,096 hours of flying in Alaska between 1966 and 1984, Amstrup *et al.* (1986) recorded 1,147 polar bear observations. Following the procedure of Scott *et al.* (1959), the approximate density of bears was 1 bear per 150 km$^2$. Amstrup *et al.* (1986) estimated polar bear densities in the Chukchi Sea to be 1 bear per 75–211 km$^2$.

Amstrup *et al.* (1986) provided a comprehensive review of polar bear sighting and mark-recapture data. From multiyear mark-recapture data they estimated a mean of 1,776 animals (SE = 274) for the Beaufort Sea population of Alaska and Canada between 1972 and 1983. Estimates ranged from 1,186 to 3,527, depending on the survival rate assumed. The estimated standard error was calculated as the square root of the sum of variances for each population estimate divided by the square of the sample size (Amstrup *et al.* 1986: table 1). The estimated density of bears in this area was 1 bear per 197 km$^2$. DeMaster *et al.* (1980) estimated a population size of 1,170–1,800 polar bears in the western Canadian Arctic, in a study area of roughly 172,000 km$^2$, using a multiyear mark-recapture technique. These data give a density estimate of 1 bear per 96–147 km$^2$. Because such estimation procedures are sensitive to changes in adult survival, they may yield less accurate estimates than it appears. Gilbert (1985) and Lentfer *et al.* (1980) reported that population estimates based on multiyear mark-recapture programs in Alaska were not reliable because it was not possible to assume that once animals left the study area they would not return (see Seber 1973:204).

Amstrup *et al.* (1986) reviewed the results of five single-season mark-recapture estimates of population size. In the first of these, Gilbert (1976, 1985) attempted to estimate numbers of polar bears in a 111-km by 111-km area north of Point Barrow. The density of bears was estimated over a 5-week period (17 March to 28 April). The Schnabel method produced an estimate of 320 bears or 250 groups (*i.e.*, an adult female with cubs is counted as one group). The Jolly–Seber method produced an estimate of 17 to 150 individuals or 13 to 45 groups. Using these estimates gives a density range of 1 bear/38 km$^2$ to 1 bear/725 km$^2$. Other single-season estimates ranged from 1 bear/129 km$^2$ to 1 bear/211 km$^2$ (Amstrup *et al.* 1986).

Amstrup *et al.* (1986) suggested that densities of polar bears in the Chukchi Sea are similar to those in the Beaufort Sea. At present, the most accepted estimate for the total population of polar bears in Alaska is 3,000–5,000 animals. The density of bears has probably never exceeded 1 bear per 137–240 km$^2$.

The only published estimates of Alaskan polar bear population trends are in Lentfer *et al.* (1980) and Amstrup *et al.* (1986). Lentfer *et al.* indicated that the population of polar bears around Point Barrow between 1967 and 1976 was increasing. This determination was based on a comparison of survival rates from a cohort of animals and from a composite age structure. Neither the variance of the survival rates nor the level of significance between the two estimates was given. In addition, the authors reported that the results of a population simulation based on the observed rates of reproduction and survival indicated that the population was increasing between 1967 and 1976. (See sections on Reproduction and Survival for a review of these data.) The rate of increase was not reported.

Amstrup *et al.* (1986) suggested that the numbers of polar bears in Alaska in 1956 and 1984 were similar. However, they indicated that the population may have declined in the late 1950s and early 1960s in response to hunting pressure, recovered during the mid- and late 1970s, and has been stable since then. Amstrup *et al.* (1986) discussed numerous possible biases and shortcomings in existing data. Disproportionate sampling of some sex and age groups and radical annual variations in small sample sizes required lumping of data in ways which could be misleading. The fact that populations in Alaska were not stable during the sampling period was also a source of possible error. Eberhardt (unpubl. data) suggested some of these problems could be reduced if only adult animals were considered. However, that approach would require a greater sampling intensity.

### Trophic Ecology

Seals are the primary prey of polar bears throughout their range, although other marine mammals, birds, and vegetative foods may also be consumed (Lono 1970, Freeman 1973, Russell 1975, Stirling and Smith 1975, Heyland and Hay 1976, Stirling and Archibald 1977). Polar bears in the Alaskan Arctic prey primarily on ringed seals (*Phoca hispida*) and to a lesser extent on bearded seals (*Erignathus barbatus*). Eley (unpubl. data) examined the remains of 71 pinnipeds killed by polar bears in Alaskan waters; 65 (93%) were ringed seals, 5 (6%) were bearded seals, and 1 was a walrus (*Odobenus rosmarus*). Bearded seals constituted 11–19% of the identifiable prey in the western Canadian Arctic (Stirling and Archibald 1977, Smith 1980). Walruses are not considered to be an important component of the polar bear diet (Kiliaan and Stirling 1978; Fay 1982; Eley, unpubl. data). Instances of polar bears killing beluga whales (*Delphinapterus leucas*) have been reported (Degerbøl and Freuchen 1935, Kleinenberg *et al.* 1964, Freeman 1973, Heyland and Hay 1976), but belugas are not considered an important component of the polar bear diet.

Stirling and Archibald (1977) reported that over 50% of ringed seals taken by polar bears on fast ice in the western Canadian Arctic and the High Arctic during periods of high ringed seal productivity were young-of-the-year. In years of low ringed seal productivity in the western Arctic, young-of-the-year ringed seals were not taken by polar bears. In addition, consumption of carcasses differed between the two study areas. The difference was thought to be related to the relative availability and productivity of ringed seals. Similar studies have not been done in Alaska.

Age-specific differences in hunting success rates have been reported by Stirling and Latour (1978) for the central Canadian High Arctic. Cubs of any age were not observed to be successful at taking seals in the spring of the year. During the summer the success rate of 2-year-olds was similar to that of adults. Young-of-the-year and yearlings were less successful than adults. The authors suggested that the poor hunting ability of cubs in the spring is related to their inability to break through the layer of snow that covers birth lairs and breathing holes at that time. They also suggested that cubs abandoned prior to the normal weaning age of 2.5 years would likely not survive.

The energetics of polar bear predation on ringed seals was discussed by Stirling and McEwan (1975), Best (1977), and Hurst *et al.* (1982). Stirling and McEwan estimated that in the Canadian Arctic 80% of ringed seals taken by polar bears are less than 2 years old. Similar studies have not been reported for Alaska. A young-of-the-year ringed seal is worth about 60,000 kcal to a polar bear. Over 70% of these calories are in fat deposits. These authors reasoned that, when seals are readily available, polar bears may eat only the skin and blubber of their prey because, at least for subadults and females with cubs, smaller animals may be interrupted at kills by larger animals. This places a premium on getting as many calories as quickly as possible from a kill. Best (1977) determined that most polar bears could consume up to 20% of their own body weight in less than 30 minutes and that, on average, a polar bear would need to kill a ringed seal every 6.4 days to maintain its body weight.

Polar bears have few natural enemies; however, walruses and wolves (*Canis lupus*) have been observed to kill polar bears. Reports of polar bears being killed by walruses are generally related to polar bears being injured, and subsequently dying, while making an unsuccessful attempt to take a walrus (Kiliaan and Stirling 1978). Wolves have been observed to take polar bear cubs in the Hudson Bay area (Ramsay and Stirling 1984), but this is thought to be uncommon in other areas because the ranges of these species generally do not overlap.

### Denning

Female polar bears enter maternity dens, which they excavate in snow, by late November; the young are born in late December or early January (Harington 1968). In most areas of the Arctic, family groups leave the dens in late March or early April. Female polar bears are quite sensitive to outside disturbances during this period (Belikov 1976, Lentfer and Hensel 1980, Amstrup 1986). Movement of bears from dens before cubs are able to walk or withstand ambient temperatures results in loss of cubs. Similarly, the successful rearing of polar bears in captivity requires a relatively undisturbed denning environment.

The density of maternity dens varies geographically (see Behavior section in DeMaster and Stirling 1981). The largest concentrations of dens are found on Wrangel Island in the Soviet Union (Uspenskii and Kistchinskii 1972), on some of the islands of the Svalbard Archipelago north of the Norwegian mainland (Larsen 1985), and near the west coast of Hudson Bay in Canada (Jonkel *et al.* 1972; Stirling *et al.* 1977*b*). Several other areas where bears consistently den have also been identified; *e.g.*, west coast of Banks Island (Stirling *et al.* 1975) and on Gateshead Island (Schweinsburg *et al.* 1984), both in Canada. In Alaska and along the western edge of Banks Island, maternity dens are thought to be sparsely distributed along the coast (Stirling *et al.* 1975, Lentfer 1976*b*, Lentfer and Hensel 1980). Lentfer and Hensel (1980) reported more dens on land and shorefast ice between the Colville River and the Canadian border than elsewhere. They suggested that this may be related to the onset of ice formation along the north coast of Alaska, which often first occurs near the Canadian border and progresses westerly. It is also probably related to the greater topographic relief found along this section of the coast. Polar bears need deep, compacted snow drifts from which they can excavate snow dens, and suitable drifts are less common on the flatter terrain of the western Arctic coast of Alaska.

Lentfer (1975) reported the first confirmed instance of polar bears denning on drifting sea ice of the Beaufort Sea. A den was found approximately 165 km from the coast in multiyear pack ice. Lentfer and Hensel (1980) reported locations on drifting ice north of Alaska of 93 litters of young-of-the-year recently out of dens. The mean distance from the coast was 77 km and the range was 7–278 km. Many had emerged from the dens so recently and were so far offshore that their dens most likely had been on the drifting ice. However, Lentfer (1975) and Lentfer and Hensel (1980) suggested several reasons why denning by polar bears on the sea ice may not be as successful as denning on land. Recent radio-tracking studies indicate that denning in multiyear pack ice in the Alaskan Beaufort Sea may be the rule and not the exception (Amstrup 1986). In the winters of 1983 and 1984, 26 radio-tagged bears were followed to maternity den sites. Only four of these sites were on land. One of the den sites was not pinpointed; the remaining 21 dens were on pack ice. In addition, several other radio-tagged bears assumed to be pregnant were last seen moving in a northerly and westerly direction in the late summer toward the multiyear pack ice. In 1985, 21 of 23 polar bears were followed to maternity den sites on pack ice (Amstrup, unpubl. data). Larsen *et al.* (1980) reported that 90% of all polar bear tracks observed in the vicinity of the FRAM I expedition (about 83°N latitude) were those of females with small cubs. Given the distance from land, it is likely that these females had also denned on multiyear pack ice.

For the 3 years 1983–86, 83% of the maternity dens found in the Alaskan Beaufort Sea were on pack ice. However, it is not clear if this was always the case or if human disturbance has altered the distribution of denning in Alaska. Stirling *et al.* (1975) suggested that Native hunters along the mainland coast of the western Canadian Arctic may have displaced polar bears from denning in this area. Leffingwell (1919) documented the removal of many bears from maternity dens along the north coast of Alaska in the early 1900s.

### Reproduction

Geographical differences in litter size, litter production, and the onset of maturity seem to exist, especially between Hudson Bay and all other populations (Stirling *et al.* 1977*b*). Therefore, estimates of these parameters from populations other than those in the Chukchi or Beaufort seas may not be reliable.

In Alaska the mean litter size of young-of-the-year, yearlings, and 2-year-olds between March and April was 1.68, 1.66, and 1.51, respectively (Lentfer 1976*b*). The litter size at birth is not known. Lentfer *et al.* (1980) reported no significant difference in litter size with age of the cubs and an average litter size of 1.63 cubs per litter ($N = 115$, SE = 0.05); data on 2-year-olds were not included. Given the discrete nature of the data and the current low level of sampling, it is unlikely that differences in litter size with age of less than 10% will ever be detected. The authors indicated that litter size may increase with the age of the female, but the age-specific sample sizes were small. DeMaster and Stirling (1983) suggested that young-of-the-year litters are not randomly sampled, because these litters are generally, and illogically, reported to be smaller than yearling litters. Lentfer *et al.* (1980) reported that females with young-of-the-year may have been undersampled because field studies started each year before emergence of females and cubs from dens. DeMaster and Stirling (1983) speculated that the average litter size at birth in Alaska is probably very close to 2.0. The median and modal litter size in Alaska, and for most populations of polar bears (excluding Hudson Bay), is 2.0. The average size in the fall for young-of-the-year litters in Alaska has not been reported, but in Canada is 1.53 (Ramsay and Stirling 1982).

The probability of parturition (defined as the proportion of mature females that are accompanied by young-of-the-year; Furnell and Schweinsburg 1984) in Alaska is 0.13 (Lentfer *et al.* 1980; referred to as "fraction which successfully bred"). This rate is the lowest reported litter production rate for polar bears and is likely an artifact of undersampling adult females with young-of-the-year. A similar bias seems to exist for the western Canadian Arctic, where the parturition rate for females 5 years old and older was 0.19 (Stirling *et al.* 1975: table 4). In both areas more yearling litters were observed than young-of-the-year litters. The parturition rate for polar bears 5 years old and older in the central Canadian Arctic was 0.31 (Furnell and Schweinsburg 1984) and in western Hudson Bay was 0.56 (Ramsay and Stirling 1982). In both of these areas the number of young-of-the-year litters was greater than the number of yearling litters.

Adult female polar bears in most areas are "available" for breeding in the spring if they are not accompanied by young-of-the-year or yearlings. Therefore, the fraction that bred successfully the preceding year can be estimated as the number of adult females with young-of-the-year divided by the number of adult females without yearlings or 2-year-olds. The resulting estimate of breeding success for polar bears 8 years old and older in Alaska is 0.34 (Lentfer *et al.* 1980: table 5); in the western Canadian Arctic, 0.61 (Stirling *et al.* 1975: table 4); and in the central Canadian Arctic, 0.67 (Furnell and Schweinsburg 1984: table 3). Breeding success of 5-, 6-, and 7-year-olds in Alaska was 0.04, 0.28, and 0.29, respectively (Lentfer *et al.* 1980); and in the central Canadian Arctic was 0.27, 0.43, and 0.58, respectively. These data are consistent with the hypothesis that females with young cubs were undersampled in the Alaskan study.

Because females with young-of-the-year are generally undersampled, age-specific estimates of the parturition rate are usually based on the number of $x$-year-old females with young-of-the-year and $x+1$-year-old females with yearlings (see Stirling *et al.* 1975 and Lentfer *et al.* 1980). Because estimates made in this manner assume that survival of cubs is near unity, which it probably is not, and the age distribution is stationary, the estimates are likely to be low. Therefore, where possible, the parturition rate should be estimated from the proportion of mature females with young-of-the-year litters (see Furnell and Schweinsburg 1984). Ramsay and Stirling (1988) discussed use of data on yearlings in estimating rates of reproduction.

A number of authors have used the reciprocal of the average number of years between breeding as an independent estimate of the rate of parturition. Lentfer (1976*b*) and Lentfer *et al.* (1980) estimated an average reproductive interval of 3.1 years ($N=8$) and 3.6 years ($N=8$), respectively, for polar bears in Alaska. Ramsay and Stirling (1982) reported an average reproductive interval of 3.2 years ($N=11$) for Hudson Bay. Taylor (pers. commun.) pointed out that using the average reproductive interval underestimates the average probability of parturition over all age classes because primaparous females are "available" for breeding at a higher rate than older females. (See Goodman [1984:167] for formula for an unbiased estimator.) However, because the fraction of females that successfully breed is an increasing function of age, the significance of the bias toward underestimation should be minimal.

Lentfer *et al.* (1980) reported an average age of first reproduction in Alaska of 6.4 years, with a range of 4–8 years. Stirling *et al.* (1975) suggested that the maximum litter production rate is not reached until age 6, but that in the western Canadian Arctic some 4- and 5-year-olds produce litters. In both of these studies, the findings may be overestimates of the true age of first reproduction because of the undersampling of females with young cubs. The onset of litter production in the central Canadian Arctic, Hudson Bay, the High Arctic, and southeast Baffin Island occurs at 5 years of age (Stirling *et al.* 1980, 1984; Ramsay and Stirling 1982; Furnell and Schweinsburg 1984). (See Ramsay and Stirling [1988] for a comprehensive review of reproductive rates of polar bears in Canada.)

The maximum reported age of reproduction for polar bears in Alaska is 18 years. The oldest bear captured or killed in Alaska was estimated to be 29 years old (Schliebe, unpubl. data). The oldest reported female with cubs in the western Canadian Arctic was 19 years old. Ramsay and Stirling (1988) concluded that reproductive senescence occurs at 20 years of age.

The mean number of female cubs produced per female per year (hereafter referred to as the reproductive rate), assuming that the adult female survives from one census period to the next, has been calculated differently by different authors. This has created problems in comparing rates of reproduction by area. Given the type of information that is available, the following estimate is proposed as being the most useful estimate of the reproductive rate [m($x$)] of an $x$-year-old female in Alaska (Eberhardt, pers. commun.):

$$m(x) = (0.5)(\text{litter size}_x)/(\text{reproductive interval}_x)$$

A range of reproductive rates for females age 8 and older in Alaska can be calculated from the following: mean litter size, 1.63 (Lentfer *et al.* 1980) and 1.98 (DeMaster and Stirling 1983); reproductive interval, 3.1 (Lentfer 1976*b*) and 3.6 (Lentfer *et al.* 1980).

Using these estimates gives a range of 0.23 to 0.32 cubs per mature female per year.

Taylor *et al.* (1986) have proposed a more detailed model for estimating age-specific rates of reproduction. The model

$$\begin{aligned} m(x) = {} & (\%\ \text{available}_{x-1}) \\ & (\text{litter production rate}_x/\text{available}) \\ & (\text{litter size}_x), \end{aligned}$$

assumes that females that lose litters of young-of-the-year and yearlings will be available to breed the following breeding season. However, because of the previously mentioned sampling biases in the Alaska data base, this model is not recommended at this time. Clearly, future data collections in Alaska must be designed to overcome current deficiencies in estimates of reproductive parameters.

**Survival**

Meaningful estimates of age-specific survival of polar bears are not available. This is because (1) estimates of survival are confounded by movements of polar bears; (2) sample sizes from mark-recapture studies are typically too small to provide sound estimates; (3) local densities of bears can fluctuate greatly from year to year (Amstrup *et al.* 1986: table 5) and, therefore, it is not possible to assume a stable age distribution or a constant population rate of change; and (4) in Alaska, monitoring of the Native harvest and collection of specimens from bears taken by Natives has not been consistent since 1972 and sample sizes have been relatively small.

Two publications report on survivorship of polar bears in Alaska. Estimates of survival by Lentfer *et al.* (1980) and Amstrup *et al.* (1986) were based on composite age-structure analysis (*i.e.*, regression analysis, Chapman–Robson). Survival estimates by Lentfer *et al.* were also based on a cohort analysis.

Lentfer *et al.* reported age- and sex-specific differences in rate of survival. Survival estimates for adult females ranged between 0.64 and 0.84. Survival estimates for adult males were similar. Survival estimates for males 2–6 years old and females 2–8 years old were between 0.69 and 0.99. The Chapman–Robson estimates were consistently less than the regression and cohort estimates. The authors stated that the cohort estimates of survival were not biased by changes in population size during the study (1967–76). According to Seber (1973) this is only true if the probability of capture is constant. If the population was increasing in the 1970s (Amstrup *et al.* 1986) and given that the number of bears captured in Lentfer *et al.*'s study did not increase significantly over time (Lentfer *et al.* 1980: table 1; $r = 0.34$, slope $= 4.68$, $P < 0.5$), the probability of capture would have been decreasing during the study period. If the number of animals captured per year was constant and if the population was increasing, an estimate of survival based on a cohort analysis is biased by the factor, 1/(discrete rate of growth). In addition, there is evidence that females with young-of-the-year may be undersampled (see Reproduction). If females aged 5 to 8 can be expected to have more young-of-the-year litters than any older age classes, then these ages would be undersampled.

Amstrup *et al.* (1986) reported a mean rate of survival for bears 1 year old and older of 0.88 (range = 0.87–0.89), which is close to estimates of the survival rate for bears in the western Canadian Arctic (DeMaster *et al.* 1980) and the central Canadian Arctic (Furnell and Schweinsburg 1984). The estimated mortality rate, 0.12, includes both natural mortality and hunting-related mortality. It is necessary to assume that the population size was constant in using a regression analysis or the Chapman–Robson method. If, as was stated previously, the population was increasing, then the estimates of survival reported by Amstrup *et al.* are negatively biased.

Survival estimates for yearlings ranged between 0.70 and 0.75 (DeMaster and Stirling 1983). This estimate was based on the change in litter size from litters of yearlings to 2-year-olds. The data were from Alaska, the western Canadian Arctic, the central Canadian Arctic, and Baffin Island.

The average annual polar bear harvest in Alaska has declined since passage of the Marine Mammal Protection Act of 1972, although there may have been a relative increase in the number of cubs and females with cubs that are taken. Between 1925 and 1953 the mean reported number of polar bear hides shipped from Alaska was 117 (Amstrup *et al.* 1986). In 1954, 1955, and 1956 the estimated annual kill was 100, 128, and 135, respectively, and 128, 250, and 162 bears were reported killed in 1958, 1959, and 1960, respectively (Amstrup *et al.* 1986).

Between 1961 and 1972 the number of polar bears taken annually in Alaska ranged from 148 to 405 and averaged 260 (Lentfer 1973, Amstrup *et al.* 1986). Seventy-five percent of these animals were males. During these years cubs and females with cubs were protected, hides and skulls had to be presented to an Alaska Department of Fish and Game agent within 30 days of the date of kill, and bag limits for sport hunters were enforced. Residents were allowed to take bears for food at any time without a permit and without limit provided aircraft were not used (Lentfer 1971*b*).

The Marine Mammal Protection Act of 1972 prohibited the hunting of polar bears in Alaska except by Alaska Natives for subsistence purposes. Under the Act the Native take was not restricted by age, sex, or number of animals, except that the take must be in a nonwasteful manner. From 1973 to 1976 an average of 45 female bears were harvested per year (Amstrup *et al.* 1986). For the years 1980–85 the reported polar bear take ranged from 89 to 292 and averaged 135 (Schliebe 1986). The harvest composition was 54% males, 30% females, and 16% unknown sex. The ratio of males to females was 64:36. The average age of the unknown-sex bears was substantially below that of animals of known sex, possibly indicating a hunter tendency to forget the sex of younger (dependent) animals. Females with cubs and their cubs comprised 16% of the harvest. Annual harvests averaged 38 animals (28%) from the Beaufort Sea and 97 animals (72%) from the Chukchi and Bering seas. The annual average age ranged from 6.2 to 10.4 for females and from 4.6 to 7.0 for males.

At present it is not possible to determine what proportion of the total mortality rate (*i.e.*, 12%) is caused by hunting. Reliable estimates of the population size and the percentage of males in the population are not available for 1960–72 when reliable information on the harvest exists. More recently, although reliable estimates of the Beaufort Sea population exist, estimates of the Native take are not exact. If the number of bears in the mainland Beaufort Sea population is 2,000 (Amstrup *et al.* 1986), and if the current harvest in this region is approximately 50 bears per year (Schliebe 1986), then harvest currently accounts for 21% of the total mortality. Losses due to crippling are thought to be low but have not been determined, and the degree to which hunting mortality and natural mortality are compensatory is unknown. New information and a more thorough analysis of the existing information are required to adequately understand the influence of hunting on polar bears in Alaska.

## MANAGEMENT

Some historical accounts suggest that Yankee whalers and subsistence hunters may have extirpated local populations of polar bears in Alaska. Prior to 1900, polar bears occupied St. Matthew Island. Unlike most of Alaska's polar bears, many of these individuals spent the summer on land instead of remaining with the sea ice as it retreated to the north. Polar bears in Hudson Bay and some parts of the Canadian Arctic archipelago still follow this lifestyle. Commercial hunters in search of seal skins and whale oil eliminated polar bears from St. Matthew Island by the early 1900s (Hanna 1920). In addition, overwintering commercial whalers along with local residents may have reduced the number of bears that once denned in the Canning River region of Alaska (Leffingwell 1919).

With the exception of the take by commercial hunters at St. Matthew Island, polar bears were taken primarily for subsistence purposes and for the sale of hides by Natives hunting with dog teams through the 1940s. Guided hunting by aircraft started in the late 1940s and continued until stopped by the State of Alaska in 1972.

In 1961 the State of Alaska made it mandatory that hunters present polar bear skins for sealing and examination. The average annual take between 1960 and 1972 was 260 animals (Lentfer 1973, Amstrup *et al.* 1986). Between 1961 and 1972 the state regulations provided a preference for subsistence hunters and protected cubs and females with cubs. During this period trophy hunters were allowed to hunt only during late winter and spring. Although some undocumented take occurred (Lentfer 1971), information on the manner of take, area of take, and age and sex composition of the known take is available for this period (Lentfer 1973).

In 1972 the Marine Mammal Protection Act vested management with the federal government. Under the Act, only Natives are allowed to take polar bears. The Act removed restrictions on the taking of cubs and females with cubs and the mandatory reporting requirement of the state's management program. The only restriction on Native take is that it must be done in a nonwasteful manner. The Act allows the federal government to restrict the take by Natives only if the polar bear population is determined to be depleted.

Most Native hunters did not become familiar with the change in management regulations for some time following the passage of the Marine Mammal Protection Act (Lentfer 1985). Therefore, cubs and females with cubs were not taken in the early 1970s to the extent that they are taken now. Several other factors also contribute to variability between years in the vulnerability of different age and sex classes of bears and the total number of animals harvested by subsistence hunters. First, the cessation of the use of aircraft for hunting polar bears may have allowed the number of animals along the coasts of Alaska to increase. Second, in some years ice conditions tend to concentrate bears along the coast. Third, an apparent tendency for females with young cubs to occupy nearshore areas during the fall makes them more vulnerable to hunting. In addition, polar bears are often attracted to carcasses of whales or other marine mammals taken by Beaufort Sea subsistence hunters. Finally, pregnant females may return to historic denning sites in the fall. These factors and unexplained variations in the availability of bears to hunters cause considerable concern about the potential for harm to polar bears in Alaska under the existing management regime.

In recognition of the polar bear's increasing vulnerability to human activities, the five nations within whose boundaries polar bears occur negotiated the

International Agreement on Conservation of Polar Bears. The Agreement, negotiated in 1973 and ratified in 1976, prohibits the taking of polar bears from aircraft or large motor vessels or in areas where they have not been taken by traditional means in the past. This prohibition creates a *de facto* sanctuary in the central Arctic basin. A resolution appended to the Agreement requests governments to prohibit the taking of cubs or females with cubs and hunting in denning areas during periods when pregnant females are moving into them or are denning. Another resolution requests governments to establish an international system of identifying hides to effectively control the trafficking of illegal hides. (See Lentfer [1974*b*] and Stirling [1986] for more comprehensive reviews.) Finally, the Agreement requires each of the signatory nations to conduct a research program and to coordinate management and research for populations that overlap jurisdictional boundaries.

Each of the five signatory nations has implemented a management program to protect polar bears and their environment. The Soviet Union ended all hunting of polar bears in 1955. The only reported taking of polar bears in the U.S.S.R. since then has been a few cubs taken each year for public display. In 1970 Norway severely reduced the taking of polar bears in the Svalbard area. In 1973 a complete ban on the taking of polar bears in Svalbard, except for defense of life and property, was established. Denmark has eliminated commercial hunting of polar bears in Greenland, and only subsistence hunting by Native residents is allowed. This hunting is further restricted by the requirement that hunters use only traditional means (which does not include motorized vehicles). In most areas of Canada female bears and their young are protected by specific statutes and by season closures. The harvest is regulated by a quota system administered cooperatively by various jurisdictions operating in each village that has access to polar bears. Reporting is mandatory. Compliance with quotas, seasons, and other biologically founded regulations is assured because of economic incentives provided by the legal sale of hides and management of a limited trophy guiding industry for maximum benefit of the local hunters and trappers. The United States chose to implement the polar bear agreement with the provisions of the Marine Mammal Protection Act. The Act, which went into effect in 1973, prohibits the hunting of polar bears by other than Indians, Aleuts, or Eskimos. However, no restrictions on the number, sex, or age of animals taken by Natives were imposed.

The current harvest monitoring program of the U.S. Fish and Wildlife Service began in November 1980 (Schliebe 1986). Twenty villages are included in the program, and each is visited monthly. Information on the age, sex, and reproductive condition of each animal taken is collected. Between 1973 and 1980, information on the harvest of polar bears in Alaska was not systematically collected. The Service has published proposed regulations which authorize mandatory reporting requirements.

Recognizing the absence of protection for female polar bears with cubs in Alaska, the Polar Bear Specialist Group affiliated with the International Union for the Conservation of Nature and Natural Resources passed a resolution in August 1985 calling for swift action among the users of polar bears in Alaska and Canada to establish voluntary restrictions that will protect female polar bears and their young. The Polar Bear Group further called for voluntary measures to be followed as soon as possible by legal protection.

Progress on the first point was made 4 April 1986 when the Fish and Game Management Committee of the North Slope Borough resolved that Alaskan hunters should not shoot cubs or females with young. This group further resolved to collaborate with the Inuit hunters of Canada to ensure that harvests of polar bears do not exceed the replacement rate of this population. Passage of the resolution was followed in September 1986 by an agreement for cooperative management between the North Slope Borough Fish and Game Management Committee and the Inuvialuit Game Council. Among other things, this cooperative management agreement calls for:

1. Establishing harvest limits
2. Protection of females and cubs
3. Protection of pregnant females
4. Protection of denning bears
5. Management system to regulate the number of polar bears harvested to comply with harvest limit allocations
6. Reporting system to collect critical information from harvested polar bears
7. Protection of important polar bear habitat

This is a positive step with the potential to afford the necessary protection of polar bears in the area of North Slope Borough jurisdiction; *i.e.*, from the Canada border westward to Cape Seppings between Point Hope and Kivalina. Similar stipulations should apply where polar bears occur outside of the North Slope Borough.

## CONSERVATION ISSUES AND DATA GAPS

The conservation of polar bears in Alaska depends primarily upon two things. First, to insure adequate space for critical life functions of feeding and reproduction, habitats of special significance to bears must be identified and protected. Second, to maintain viable polar bear populations, human activities that directly or indirectly alter the numbers of polar bears occupying available habitat must be controlled. To determine the effectiveness of programs designed to protect critical habitats and to control human activities, monitoring programs must be developed and implemented.

### Habitat Preservation

The mobility of polar bears combined with the fact that much of their habitat consists of sea ice results in unusual problems in identifying important habitat. The most obvious and identifiable habitats important to polar bears are maternity denning areas because reproductive effort there can most easily be altered. Areas where open water or active ice persists through the winter and early spring are important habitats for feeding.

The potential to adversely impact denning bears due to disturbance in or around dens has been demonstrated (Stirling *et al.* 1975, Belikov 1976, Lentfer and Hensel 1980). The actual degree to which denning polar bears in Alaska are disturbed is not known at this time. This is partly related to the unknown significance of pack ice denning. Lentfer and Hensel (1980) reported locations of 35 dens, 5 on drifting ice and 30 on land or shorefast ice. They also reported a significant number of newborn cubs so far from land that they likely emerged from dens on drifting ice. More recently, only 17% ($N = 76$) of dens located in Alaska by radiotelemetry were on land. Concern has been raised over the potential for displacing females from historically important denning areas by either hunting or industrial activity (Stirling *et al.* 1984). It is therefore critical to determine the significance of offshore denning and how successful such denning is relative to onshore denning.

Less is known about habitat preference for polar bear feeding than is known about denning, but it seems clear that individual bears show a great deal of site fidelity at certain times of the year. The importance of polynyas, areas where ice consistently breaks up and makes open water and newly refrozen areas available for much of the winter, is well established (Stirling and Cleator 1981). In general, areas that contain polynyas may be the most important marine habitats in the Arctic (Stirling and Cleator 1981). Recent studies have shown that polar bears spend the majority of their time in a band extending from the shore leads that parallel the coast of Alaska out to approximately 200 km offshore. The ice in this zone is generally more active and has more open water and refreezing areas than either shorefast ice or heavy pack ice to the north. The effect of human activities, such as seismic exploration or shipping, in these areas on either polar bears or their prey is unknown. In addition, concern has been expressed that contamination of ice, water, food species, and bears themselves by oil or other toxic chemicals may increase as human activities increase in the Arctic over the next few decades. (See Stirling and Calvert [1983] for a comprehensive review.) Acute exposure to such compounds can be fatal (Øritsland *et al.* 1981). However, the long-term effects of lower levels of such contamination are not known (Stirling and Calvert 1983).

### Nonconformance to Polar Bear Agreement

Under the current management regime an unlimited number of polar bears, of any age and either sex, may be taken by Native hunters. As stated earlier, Native hunters of the North Slope Borough may voluntarily restrict the taking of cubs or females with cubs. It is not clear if hunters from the west coast of Alaska (*i.e.*, outside of the North Slope Borough) will voluntarily protect cubs and females with cubs. Currently there are no seasonal or area closures to protect pregnant females as recommended by the Agreement on Conservation of Polar Bears. The status of implementing mandatory reporting requirements is unclear. Therefore, though moving in the right direction, the U.S. management program for polar bears is not in compliance with the Polar Bear Agreement.

Canada has developed a quota system by village. The taking of cubs and females with cubs is banned, and seasonal closures protect pregnant females. The maximum allowable take has been estimated to equal 5% of the local population per year. Taylor *et al.* (1986) determined that a population of 4,000 animals (roughly the size of the polar bear population in Alaska) can sustain a harvest of no more than 80 adult females per year. Amstrup (1986) estimated that for the Beaufort Sea population as few as 56 adult females may be recruited into the population each year.

The average polar bear harvest in Alaska has declined since passage of the Marine Mammal Protection Act. However, available evidence indicates, at least for the Beaufort Sea population, that the annual loss of females is currently about the maximum allowable. The recently passed resolution of the North Slope Borough recommending against the taking of cubs or females with cubs may reduce their vulnerability. However, a mandatory harvest monitoring program for all villages is needed to verify the number, sex, age, and location of bears taken. In addition, efforts to convey biological concepts to user groups must be expanded.

### Population Discreteness

Recent evidence indicates that polar bears north of Alaska and in the western Canadian Arctic constitute a single management unit. The degree of separation between bears in Alaska and the U.S.S.R. is not known at this time. Given the current level of take by Natives in Alaska and Canada, it is essential that management of polar bears in the Beaufort Sea be coordinated between the two countries. Moreover, because there may be limited movement of animals between the Beaufort and Chukchi seas, the significance of such movements must be determined. It is likely that such movements are associated with unusual weather conditions and, therefore, research programs will have to be designed to accommodate the variability in annual ice conditions.

### Interactions with People

Polar bears sometimes pose a threat to or attack people living and working in the Arctic (Schweinsburg 1976, Guravich 1980), and this often results in bears being killed. Stenhouse (1983) and Bromley (1985) summarized ways to minimize bear–human interactions. Camps should not be located in areas of active ice, near shore leads, or on points of land where ocean currents might deposit carcasses of marine mammals. Food and garbage in camps and villages should be handled so as not to attract bears. Workers new to the Arctic should be indoctrinated on bear behavior and procedures to use if confronted by a bear. A bear that comes into a camp or settlement should not be allowed to become habituated and lose fear of humans, but should be thoroughly frightened and, if possible, driven several kilometers away with a snow machine or helicopter. Close encounters can be prevented by use of trip-wire alarm systems and tied dogs which bark at the sight or scent of bears. Efforts should continue to develop reliable, nonlethal methods to deter bears.

### Monitoring Programs

The effectiveness of a management program in controlling the adverse effects of human activities on polar bears in Alaska can only be evaluated relative to specific management goals, *e.g.*, to maintain the population at or above the level of maximum net productivity. The population is currently thought to be within this range. However, techniques sensitive enough to detect other than very large changes in the size of the Alaskan population have not been developed. Traditional survey approaches have proven unreliable and expensive because of the low density of bears on the sea ice. Mark-recapture programs are expensive and slow to provide information on changes in population size. Catch per unit effort indices of abundance have lacked suitable precision to be reliable. The U.S. Fish and Wildlife Service is currently trying to develop a survey technique that takes advantage of weather conditions that tend to concentrate animals in a relatively narrow band offshore. Such a survey may take place only once every few years, but may provide an adequate basis for evaluating the effectiveness of various management activities. Before any type of population monitoring program is adopted it should be evaluated in terms of what level of change could be detected, given a particular level of effort (Holt *et al.* 1986).

## MANAGEMENT RECOMMENDATIONS

*1) Manage in Conformity with Polar Bear Agreement.*—Simulation models suggest polar bear populations are extremely sensitive to harvesting of adult females. In addition, pregnant or post-parturient polar bears often occur closer to human settlements than other components of the population. Cubs and females with cubs, therefore, need greater protection than other age and sex classes. The current North Slope Borough resolution recommending against the taking of cubs or females with cubs is a positive step. The recommendation should be extended to villages outside the jurisdiction of the North Slope Borough. In addition, fall hunting should be restricted to protect pregnant females returning to traditional denning areas. Females and cubs in dens should be protected. Efforts to minimize disturbance from hunting and industrial activities in areas critical for denning and feeding should be continued and, where necessary, increased.

*2) Monitor Changes in Population Size.*—Industrial activities and hunting may adversely affect polar bears in Alaska. Therefore, it is necessary to monitor changes in population size over time. Present survey techniques cannot provide a valid index of abundance. Ongoing research efforts must lead to the development of new survey methodologies. Once developed, surveys should be conducted on a regular basis.

*3) Make Harvest Reporting Mandatory.*—Because polar bear populations are sensitive to the removal of adult females, sex and age composition and size of the harvest must be known in order to determine whether a particular level of harvest will adversely affect a population of polar bears. This is best done by a mandatory reporting program whereby hunters are required to present hides for sex determination and skulls for measurements and collection of a tooth. The responsible management agency should be required to analyze and report results of the previous year's harvest monitoring program within the first 6 months of the following year.

*4) Reduce Bear–Human Interactions.*—The nature, magnitude, and trend of bear-human interactions over the past 20 years should be determined.

Education programs should be implemented in problem areas. When bears are killed as nuisance animals, the agency responsible for management should review the circumstances. The effectiveness of available detection and deterrent systems for Alaska must be evaluated. Efforts to develop more reliable deterrents should continue. These activities should be coordinated with those of the Northwest Territories, Canada.

***5) Protect Polar Bear Habitat and Populations.***—Several agencies of the state and federal governments have resource management responsibilities that can affect polar bear habitat and populations. Land and ocean activities should be regulated and other management activities coordinated and conducted so that polar bear habitat and populations are not adversely affected.

## RESEARCH RECOMMENDATIONS

In order to be most effective, future polar bear research must proceed in the following order. First, the populations in question must be defined. One cannot discuss population size, trend, or other population parameters until one knows what the population is. Then, the important parameters such as survival, recruitment, and age composition must be determined. Distribution patterns and feeding and other behaviors must also be understood because they may introduce bias into estimates of life history parameters. Finally, survey and index techniques that take these considerations into account can be developed. Specific research recommendations and suggestions are as follows.

***1) Define the Populations In and Adjacent to Alaska.***—Information on the degree to which polar bears in the eastern and western Beaufort Sea and the Chukchi and Beaufort seas mix indicates that animals in the former, but not the latter, constitute a single management unit. Therefore, management agencies in the United States and Canada must coordinate their individual management strategies to conserve polar bears in this area. At present, however, there is insufficient information to determine the degree to which animals in the Beaufort and Chukchi seas constitute discrete stocks. Therefore, telemetry studies should be expanded to include instrumenting and tracking an adequate sample of animals in the Chukchi and Bering seas and at the interface of the Beaufort and Chukchi seas.

In addition to telemetry studies, the feasibility of using levels of contamination of various pollutants to define stock discreteness should be tested. Initial studies by Lentfer (1976*a*, 1987) were informative, but recent refinements in this approach need to be incorporated into a research project. Specimen material can be easily obtained as part of the harvest monitoring program. Therefore, the only significant cost of such a project would be for the chemical analysis.

Analyses of nuclear and mitochondrial DNA can also be used to define population discreteness. The U.S. Fish and Wildlife Service is currently testing the value of such analyses, as well as investigating the potential for using different types of algae that are found in the hair of polar bears to augment other studies on stock discreteness of Alaskan polar bears.

***2) Describe Relationships between Polar Bears, Seals, and Sea Ice.***—Distribution of polar bears is tied closely to the condition and distribution of sea ice. However, effects of ice drift patterns, topography, and lead development on polar bear movements and distribution are not clearly understood. In order to understand the movements and distribution of polar bears well enough that meaningful surveys of population trend and size can be conducted, the relationships between polar bears and movements and condition of ice must be better understood. Therefore, information on ice formation, movement, and distribution should be obtained, along with information on polar bear movements and activities. Correlations between polar bears and sea ice should then be developed.

Also not understood are predator-prey relationships between polar bears and their principal food species—ringed seals and bearded seals. Distribution and abundance of ringed seals in different ice types are not well known, nor is the manner in which polar bears hunt seals in the various kinds of ice. Some information obtained under laboratory conditions on dietary requirements of polar bears, when combined with ringed seal population estimates, suggests that estimated numbers of polar bears could require more seals than are available. There is clearly a need to describe relationships between polar bears, seals, and sea ice as a basis for understanding polar bear ecology and designing meaningful population and trend surveys.

***3) Refine Population Parameters.***—Detecting significant trends in polar bear abundance, reproduction, and survival, if possible, will likely require a time series of at least 8 or 10 years (Gerrodette 1987). Therefore, to avoid unnecessary population declines, population monitoring will have to be augmented by projecting population trends from current estimates of various life history parameters and harvest data, including total kill and age and sex composition. At a minimum, information on the average reproductive interval, the recruitment rate to age 6, and the adult survival rate are needed. With improved information on these life history parameters, existing models can be used to predict how the population will change over the next few years and how a particular change in management strategy might affect this projection. At this point, polar bear management lacks adequate information, not an adequate model to analyze the data. Concurrent with this analysis should be a sensitivity analysis of the modeling results.

At present, satellite telemetry offers the most promising approach to understanding the population dynamics of polar bears in Alaska. Ideally, recently emerged adult females with young-of-the-year or females with 2-year-olds could be radio-tagged and followed over time until the reproductive cycle has been completed. Such an approach will provide data on the reproductive interval, cub survival, and adult survival, as well as information on important habitats and movement patterns. A preliminary analysis will be necessary to determine what sampling level provides adequate precision. The U.S. Fish and Wildlife Service is currently conducting and plans to continue research to refine population parameters.

Eberhardt's (pers. commun.) recent analysis of the available information on the population dynamics of Alaskan polar bears indicates that females in Alaska have lower rates of parturition, an older age of first reproduction, and a smaller average litter size than do populations of polar bears in Canada. The reasons for these differences are not obvious. For example, Lentfer *et al.* (1980) suggested that young cubs were undersampled in the first few years of their study. It is possible that this bias could be removed by a number of stratification strategies. In addition, DeMaster (pers. commun.) performed a preliminary analysis of the Alaskan polar bear data base in 1980 and found over 20 cases where the length of the reproductive interval could be estimated from information on the presence or absence of cubs. Eberhardt reported that the adult rate of survival required to produce a stationary population level is at least 0.975, given various rates of recruitment. An adult survival rate of 0.975 or greater may be unrealistic; yet Amstrup *et al.* (1986) suggested that polar bear populations in the 1970s were probably increasing in Alaska and are currently likely to be stable. Therefore, a comprehensive analysis of the existing information should be undertaken to determine the likelihood of sampling biases in the data, geographic differences in various life history parameters, or long-term trends in the population.

***4) Determine Significance of Denning on Pack Ice.***—Radio-tracking is providing insight into the potential significance of denning on pack ice. However, the suitability of pack-ice denning relative to mainland denning has not been determined. Telemetry studies should continue over the next few years to determine areas critical to successful denning.

Telemetry studies should be expanded to determine the degree to which human activities such as shipping may disrupt animals denning in the pack ice. If it is found that denning on pack ice is significantly less successful than denning on land, research should immediately be directed toward determining the factors that may be responsible for the abandonment of what may have been traditional denning habitat on land.

***5) Develop Index of Population Abundance.***—After population boundaries have been defined, methods for assessing trends in the population should be developed. The U.S. Fish and Wildlife Service started research in fiscal year 1986 to develop an index of population abundance. A number of possible methods have been tested, but so far none have proven both practical and reliable. It is probable that knowledge gained from telemetry and tagging studies could be used to develop more efficient survey techniques. In fiscal year 1987 the Service began testing the feasibility of line and strip transect surveys from fixed-wing aircraft when bears are concentrated along a relatively narrow band of active ice because of weather conditions. If one of these survey methods appears promising, the level of population change that can be detected relative to a given level of effort should be determined. A panel of experts should be convened to review proposed methodology.

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## REFERENCES CITED

AMSTRUP, S. C.
1986. Research on polar bears in Alaska, 1983–1985. Pages 85–115 *in* Polar bears: Proceedings of the Ninth Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 9–11 August 1985, Edmonton, Alberta, Canada. Int. Union Conserv. Nature and Nat. Resour., Gland, Switzerland.

AMSTRUP, S. C., I. STIRLING, AND J. W. LENTFER.
1986. Past and present status of polar bears in Alaska. Wildl. Soc. Bull. 14(3):241–254.

BELIKOV, S. E.
1976. Behavioral aspects of the polar bear, *Ursus maritimus.* Pages 37–40 *in* M. R. Pelton, J. W. Lentfer, and G. E. Folk, eds. Bears—their biology and management. IUCN Publ. New Ser. 40.

Best, R. C.
1977. Ecological aspects of polar bear nutrition. Pages 203–211 *in* R. L. Phillips and C. Jonkel, eds. Proceedings of the 1975 Predator Symposium. Univ. Montana, Missoula.

Bromley, M.
1985. Safety in bear country: a reference manual. Northwest Territ. Dep. Renewable Resour. 24pp.

Degerbøl, M., and P. Freuchen.
1935. Mammals. Rep. 5th Thule Exped. 1921–24, 2(4–5):109.

DeMaster, D. P., M. C. S. Kingsley, and I. Stirling.
1980. A multiple mark and recapture estimate applied to polar bears. Can. J. Zool. 58:633–638.

DeMaster, D. P., and I. Stirling.
1981. *Ursus maritimus.* Mamm. Species 145:1–7.
1983. The estimation of survival and litter size of polar bear cubs. Int. Conf. Bear Res. Manage. 5:260–263.

Eberhardt, L. L.
1978. Appraising variability in population studies. J. Wildl. Manage. 42:207–238.

Fay, F. H.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N. Am. Fauna 74. 279pp.

Frame, G. W.
1969. Occurrence of polar bears in the Chukchi and Beaufort seas, summer, 1969. J. Mammal. 53: 187–189.

Freeman, M. M. R.
1973. Polar bear predation on beluga in the Canadian Arctic. Arctic 26:163–164.

Furnell, D. J. and R. E. Schweinsburg.
1984. Population dynamics of central Canadian Arctic island polar bears. J. Wildl. Manage. 48(3): 722–728.

Gerrodette, T.
1987. A power analysis for detecting trends. Ecology 68(5):1364–1372.

Gilbert, J. R.
1976. Single season estimates of polar bear numbers using mark-resighting methods. Internal rep., U.S. Fish and Wildl. Serv., Denver Wildl. Res. Center, Denver, Colo. 17pp.
1985. Evaluation of methods to estimate polar bear population size. Unpubl. manuscr., U.S. Fish and Wildl. Serv., Anchorage, Alaska. 18pp.

Goodman, D.
1984. Statistics of reproductive rate estimates, and their implications for population projection. Reproduction in whales, dolphins and porpoises. Int. Whaling Comm., Spec. Issue 6:161–174.

Guravich, D.
1980. Protecting bear and man in the Arctic. Exxon 19(3):16–21.

Hanna, G. D.
1920. Mammals of the St. Matthew Islands, Bering Sea. J. Mammal. 1:118–122.

Harington, C. P.
1968. Denning habits of the polar bear. Can. Wildl. Serv. Rep. 5:1–30.

Heyland, J. D., and K. Hay.
1976. An attack by a polar bear on a juvenile beluga. Arctic 29:56–57.

Holt, R. S., T. Gerrodette, and J. B. Cologne.
1986. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific 1986–1990. Internal rep., U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Center, La Jolla, Calif. 20pp.

Hurst, R. J., M. L. Leonard, P. D. Watts, P. Beckerton, and N. A. Øritsland.
1982. Polar bear locomotion: body temperature and energetic cost. Can. J. Zool. 60:40–44.

Jonkel, C. J., G. B. Kolenosky, R. J. Robertson, and R. H. Russell.
1972. Further notes on polar bear denning habits. Pages 142–158 *in* S. Herrero, ed. Bears—their biology and management. IUCN Publ. New Ser. 23.

Kiliaan, H. P. L., and I. Stirling.
1978. Observations on overwintering walruses in the eastern Canadian High Arctic. J. Mammal. 59:197–200.

Kleinenberg, S. E., A. V. Yablokov, B. M. Bel'kovich, and M. N. Tarasevich.
1964. Beluga (*Delphinapterus leucas*): investigation of the species. Akad. Nauk SSSR, Moscow. 454pp. (Transl. from Russian by Israel Prog. Sci. Transl., 1969, 376pp. Avail. Natl. Tech. Inf. Serv., TT67-51345.)

Larsen, T.
1985. Polar bear denning and cub production in Svalbard, Norway. J. Wildl. Manage. 49:320–326.

Larsen, T., C. Jonkel, and C. Vibe.
1980. Satellite radio-tracking of polar bears between Svalbard and Greenland. Int. Conf. Bear Res. Manage. 5:230–237.

Leffingwell, E.
1919. The Canning River region, northern Alaska. U.S. Geol. Surv. Prof. Pap. 109. U.S. Gov. Print. Off., Washington, D.C. 247pp.

Lentfer, J. W.
1971*a*. Polar bear report. Alaska Dep. Fish and Game, Pittman-Robertson Proj. Rep. W-17-4 and W-17-5. 22pp.
1971*b*. The effects of ocean currents and ice movement on polar bear activity. Alaska Dep. Fish and Game, Pittman-Robertson Proj. Rep. W-17-2 and W-17-3. 11pp.
1972. Polar bear—sea ice relationships. Pages 165–171 *in* S. Herrerro, ed. Bears—their biology and management. IUCN Publ. New Ser. 23.
1973. Polar bear report. Alaska Dep. Fish and Game, Pittman-Robertson Proj. Rep. W-17-4 and W-17-5. 24pp.
1974*a*. Discreteness of Alaskan polar bear populations. Proc. Int. Congr. Game Biol. 11:323–329.
1974*b*. Agreement on conservation of polar bears. Polar Record 17(108):327–330.
1975. Polar bear denning on drifting sea ice. J. Mammal. 56:716–718.
1976*a*. Environmental contaminants and parasites in polar bears. Alaska Dep. Fish and Game, Pittman-Robertson Proj. Rep. W-17-4 and W-17-5. 22pp.

1976*b*. Polar bear reproductive biology and denning. Alaska Dep. Fish and Game, Pittman-Robertson Proj. Rep. W-17-3 and W-17-4. 22pp.

1983. Alaskan polar bear movements from mark and recovery. Arctic 36(3):282-288.

1985. The polar bear. Pages 27-36 *in* J. J. Burns, K. J. Frost, and L. F. Lowry, eds. Marine mammals species accounts. Alaska Dep. Fish and Game Tech. Bull. 7.

1987. Mercury in polar bears from Alaska. J. Wildl. Dis. 23:338-341.

Lentfer, J. W., and R. J. Hensel.

1980. Alaskan polar bear denning. Pages 101-108 *in* C. J. Martinka and K. L. McArthur, eds. Bears—their biology and management. Fourth International Conference on Bear Research and Management. U.S. Gov. Print. Off., Washington, D.C.

Lentfer, J. W., R. J. Hensel, J. R. Gilbert, and F. E. Sorensen.

1980. Population characteristics of Alaskan polar bears. Pages 102-115 *in* C. J. Martinka and K. L. McArthur, eds. Bears—their biology and management. Fourth International Conference on Bear Research and Management. U.S. Gov. Print. Off., Washington, D.C.

Lono, O.

1970. The polar bear (*Ursus maritimus* Phipps) in the Svalbard area. Nor. Polarinst. Skr. 149. 103pp.

Manning, T. H.

1971. Geographical variation in the polar bear, *Ursus maritimus* Phipps. Can. Wildl. Serv. Rep. 13. 27pp.

Øritsland, N. A., F. R. Engelhardt, F. A. Juck, R. J. Hurst, and P. D. Watts.

1981. Effect of crude oil on polar bears. Environmental Studies No. 24. Northern Affairs Program, Northern Environmental Protection Branch, Indian and Northern Affairs, Canada. 268pp.

Papanin, I.

1939. Life on an ice-floe. Hutchinson, London. 240pp.

Ramsay, M. A., and I. Stirling.

1982. Reproductive biology and ecology of female polar bears in western Hudson Bay. Nat. Can. (Que.) 109:941-946.

1984. Interactions of wolves and polar bears in northern Manitoba. J. Mammal. 65(4):693-694.

1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). J. Zool. (Lond.): in press.

Ray, C. E.

1971. Polar bear and mammoth on the Pribilof Islands. Arctic 24:9-19.

Russell, R. H.

1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic 28:117-129.

Schliebe, S. L.

1986. Alaska polar bear Native subsistence harvest, 1980-1985. Pages 117-131 *in* Polar bears: Proceedings of the Ninth Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 9-11 August 1985, Edmonton, Alberta, Canada. Int. Union Conserv. Nature and Nat. Resour., Gland, Switzerland.

Schweinsburg, R. E.

1976. More research needed to minimize conflicts between men and polar bears. Oilweek 15:54-55.

Schweinsburg, R. E., W. Spencer, and D. Williams.

1984. Polar bear denning area at Gateshead Island, N.W.T. Arctic 37(2):169-171.

Scott, R. F., K. W. Kenyon, J. L. Buckly, and S. T. Olson.

1959. Status and management of the polar bear and Pacific walrus. Trans. N. Am. Wildl. Conf. 24:366-373.

Seber, G. A. F.

1973. The estimation of animal abundance. Hafner Press, New York. 506pp.

Smith, T. G.

1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Can. J. Zool. 58(12): 2201-2209.

Stefansson, V.

1921. The friendly Arctic. Macmillan, New York. 361pp.

Stenhouse, G.

1983. Bear detection and deterrent study, Cape Churchill, Manitoba. N.W.T. Wildl. Serv. File Rep. 44. 59pp.

Stirling, I.

1986. Research and management of polar bears, *Ursus maritimus*. Polar Record 23(143):167-176.

Stirling, I., D. Andriashek, and W. Calvert.

1981. Habitat preferences and distribution of polar bears in the western Canadian Arctic. Final rep. to Dome Petroleum Ltd., Esso Resources Canada Ltd., and Canadian Wildlife Service. 49pp.

Stirling, I., D. Andriashek, P. Latour, and W. Calvert.

1975. The distribution and abundance of polar bears in the eastern Beaufort Sea. Dep. Environ., Victoria, B.C., Beaufort Sea Tech. Rep. 2. 59pp.

Stirling, I., and W. R. Archibald.

1977. Aspects of predation of seals by polar bears. J. Fish. Res. Board Can. 34(8):1126-1129.

Stirling, I., W. R. Archibald, and D. P. DeMaster.

1977*a*. Distribution and abundance of seals in the eastern Beaufort Sea. J. Fish. Res. Board Can. 34:976-988.

Stirling, I., and W. Calvert.

1983. Environmental threats to marine mammals in the Canadian Arctic. Polar Record 21(134):433-449.

Stirling, I., W. Calvert, and D. Andriashek.

1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. Can. Wildl. Serv. Occas. Pap. 44. 32pp.

1984. Polar bear (*Ursus maritimus*) ecology and environmental considerations in the Canadian High Arctic. Pages 201-222 *in* R. Olson, F. Geddes, and R. Hastings, eds. Northern ecology and resource management. Univ. Alberta Press, Edmonton.

Stirling, I. and H. Cleator.

1981. Polynyas in the Canadian Arctic. Can. Wildl. Serv. Occas. Pap. 45. 73pp.

Stirling, I., C. Jonkel, P. Smith, P. Robertson, and D. Cross.

1977*b*. The ecology of the polar bear along the western coast of Hudson Bay. Can. Wildl. Serv. Occas. Pap. 33. 69pp.

STIRLING, I., AND P. B. LATOUR.
1978. Comparative hunting abilities of polar bear cubs of different ages. Can. J. Zool. 56(8):1768–1772.

STIRLING, I., AND E. H. MCEWAN.
1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. Can. J. Zool. 53:1021–1027.

STIRLING, I., AND T. G. SMITH.
1975. Interrelationships of Arctic Ocean mammals in the sea ice habitat. Proc. Circumpolar Conf. North. Ecol. (Ottawa, Can.) 2:129–136.

TAYLOR, M. K., D. P. DEMASTER, F. L. BUNNELL, AND R. E. SCHWEINSBURG.
1986. Sustainable harvest of polar bears (*Ursus maritimus*). Internal rep., Wildl. Serv., Yellowknife, Northwest Territ.

TOVEY, P. E., AND R. F. SCOTT.
1957. A preliminary report on the status of polar bears in Alaska. Unpubl. manuscr., U.S. Fish and Wildl. Serv. 11pp. [8th Science Conf., Anchorage, Alaska.]

USPENSKII, S. M., AND A. A. KISTCHINSKII.
1972. New data on the winter ecology of the polar bear (*Ursus maritimus*) on Wrangel Island. Pages 181–197 *in* S. Herrero, ed. Bears—their biology and management. IUCN Publ. New Ser. 23.

WILSON, D. E.
1976. Cranial variation in polar bears. Pages 447–453 *in* M. R. Pelton, J. W. Lentfer, and G. E. Folk, eds. Bears—their biology and management. IUCN Publ. New Ser. 40.

## PERSONAL COMMUNICATIONS AND SOURCES OF UNPUBLISHED DATA

T. J. Eley, U.S. Fish and Wildlife Service, Anchorage, Alaska.

J. W. Lentfer, Polar Bear Project Leader (retired), Alaska Department of Fish and Game, Juneau, Alaska.

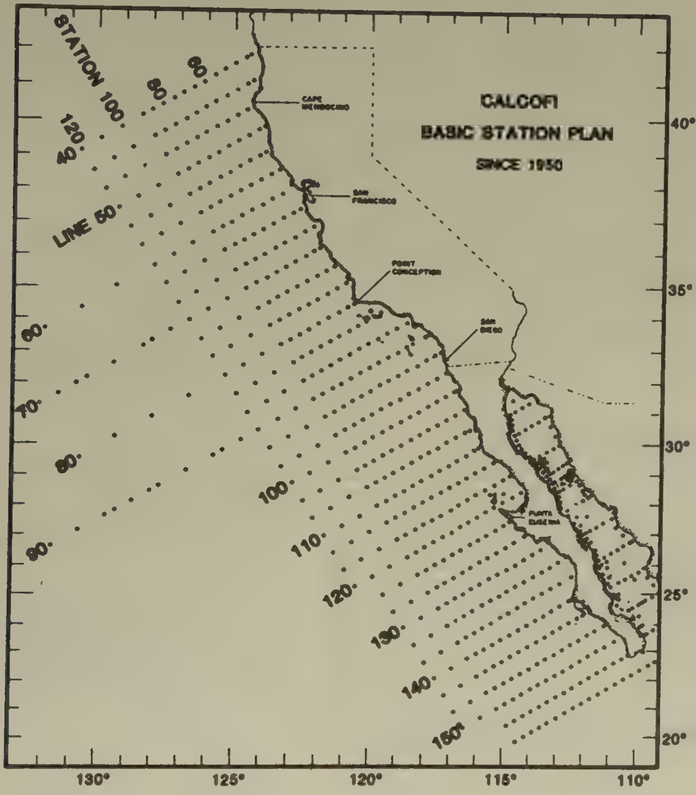
S. L. Schliebe, U.S. Fish and Wildlife Service, Anchorage, Alaska.

M. K. Taylor, Northwest Territories Wildlife Service, Yellowknife, N.W.T., Canada.

8805

# CalCOFI ON-LINE DATA SYSTEM USER'S MANUAL

**National Oceanic and Atmospheric Administration**
National Marine Fisheries Service
Southwest Fisheries Center


STATION
60
80
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LINE 50
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
CALCOFI
BASIC STATION PLAN
SINCE 1950
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30°
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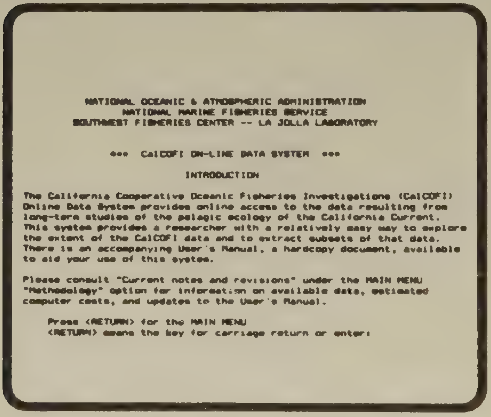
130°
125°
120°
115°
110°

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) is a consortium of marine research institutions engaged in long-term studies of the pelagic ecology of the California Current. In support of these studies, systematic surveys have been conducted since 1951; approximately 50,000 plankton samples and 20,000 hydrocasts have been obtained during the course of over 300 cruises.

The CalCOFI On-Line Data System provides on-line access to the data resulting from analyses of the plankton and water samples. This system provides a researcher with a relatively easy way to explore the extent of the CalCOFI data and to extract subsets of that data. The ichthyoplankton portion of this system is an electronic edition of the data report series published by the Southwest Fisheries Center in 1987 and 1988. This report series is the authoritative and citable source of the CalCOFI ichthyoplankton data. Any researcher using this system is strongly encouraged to consult the data reports (cited in the on-line reference list) for the most complete description of these data.

## REQUIRED HARDWARE AND SIGN-ON/SIGN-OFF PROCEDURES

*The CalCOFI On-line Data System is maintained in a VAX/VMS computing environment. The system currently resides on a VAX/780 computer operated by the UCSD Academic Computing Center (designated SDCC1) and accessed through the UCSD Local Area Network. For accounting purposes, any researcher desiring access to the system must have an account on SDCC1 or use a special account set up by Information Technology Services at the Southwest Fisheries Center. Once logged on SDCC1, type @CALCOFI at the $ prompt to bring up the INTRODUCTION.*



```
           NATIONAL OCEANIC & ATMOSPHERIC ADMINISTRATION
                  NATIONAL MARINE FISHERIES SERVICE
          SOUTHWEST FISHERIES CENTER -- LA JOLLA LABORATORY


               ***  CalCOFI ON-LINE DATA SYSTEM  ***

                            INTRODUCTION

The California Cooperative Oceanic Fisheries Investigations (CalCOFI)
Online Data System provides online access to the data resulting from
long-term studies of the pelagic ecology of the California Current.
This system provides a researcher with a relatively easy way to explore
the extent of the CalCOFI data and to extract subsets of that data.
There is an accompanying User's Manual, a hardcopy document, available
to aid your use of this system.

Please consult "Current notes and revisions" under the MAIN MENU
"Methodology" option for information on available data, estimated
computer costs, and updates to the User's Manual.

    Press <RETURN> for the MAIN MENU
    <RETURN> means the key for carriage return or enter:
```

*Output is directed to both the terminal screen and to a computer file for subsequent processing or printing. Terminal display can be prematurely aborted without affecting the integrity of the computer file. Output file formats are described in the on-line methodology section. Screen display of 132-column tables requires VT100 terminal emulation. Screen display of plots requires Tektronix 4010/14 graphics capability. Plot files are not saved.*

*The system is capable of servicing one researcher at a time. If the system is in use access will be denied and the researcher will be advised to try again at a later time. The researcher signs off through the main menu. The system responds by displaying the computer charges and the names and formats of output files created during the on-line session.*

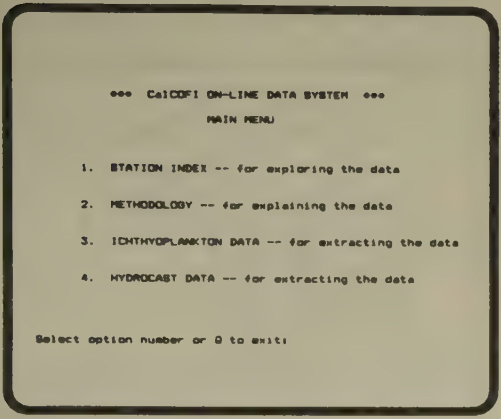
*For additional information contact:*

CalCOFI Data Manager
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038
(619) 546-7157

**CalCOFI Online Data System**
**Version 1.0**
**April 1988**

## MAIN MENU

The main menu provides the researcher with options that describe the extent of the observations, the methods used to collect and process the samples, horizontal distributions of ichthyoplankton data, and vertical profiles of temperature, salinity and oxygen content.



```
*** CalCOFI ON-LINE DATA SYSTEM ***
            MAIN MENU

1.  STATION INDEX -- for exploring the data

2.  METHODOLOGY -- for explaining the data

3.  ICHTHYOPLANKTON DATA -- for extracting the data

4.  HYDROCAST DATA -- for extracting the data


Select option number or 0 to exit:
```

**1. STATION INDEX** is chosen to explore the extent of the data and to note the cruise numbers and geographic areas of interest. These will be required as input for data extraction.

**2. METHODOLOGY** option provides access to an on-line document that describes the ichthyoplankton sampling protocol and sorting procedures. Descriptions of the output files and an annotated list of references are also available.

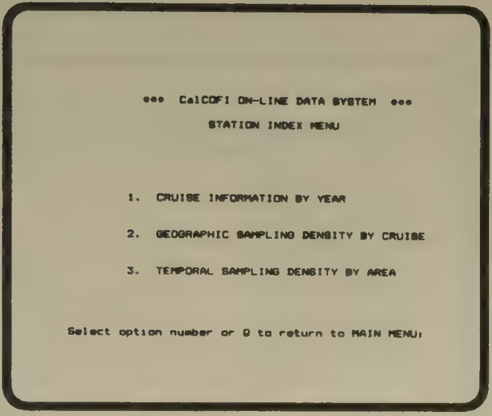
**3. ICHTHYOPLANKTON DATA** option is chosen to extract counts of fish eggs and larvae. The researcher is asked to specify the desired cruises.

**4. HYDROCAST DATA** option is chosen to extract estimates of temperature, salinity and oxygen at standard depths. The researcher is asked to specify the desired cruises.

Each option from the main menu has an associated submenu. These are described on the following pages.

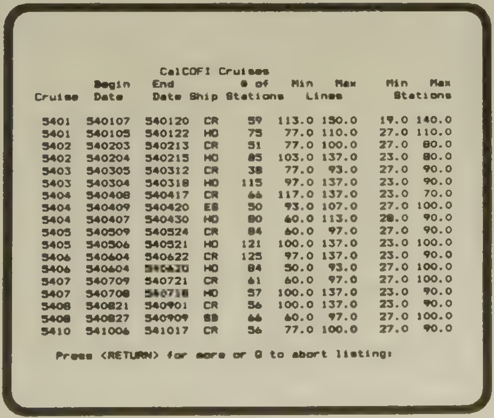
## 1. STATION INDEX

**Station Index** provides an overview of the geographic and temporal sampling density. It is intended to be used as an aid in specifying criteria for data selection.



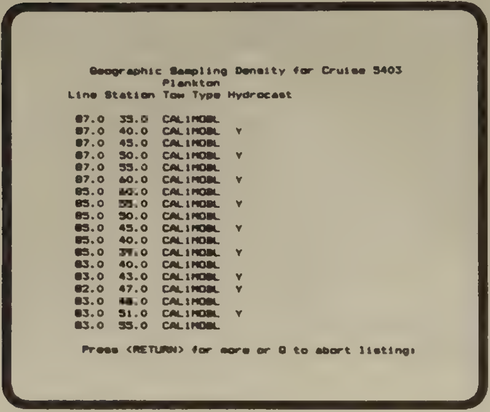
```
*** CalCOFI ON-LINE DATA SYSTEM ***
        STATION INDEX MENU


1.  CRUISE INFORMATION BY YEAR

2.  GEOGRAPHIC SAMPLING DENSITY BY CRUISE

3.  TEMPORAL SAMPLING DENSITY BY AREA


Select option number or 0 to return to MAIN MENU:
```

**1.1 CRUISE INFORMATION BY YEAR** option provides the beginning and ending dates of every cruise, the name of the ship(s) used, and the number of stations occupied for the year(s) specified. Typical screen output:



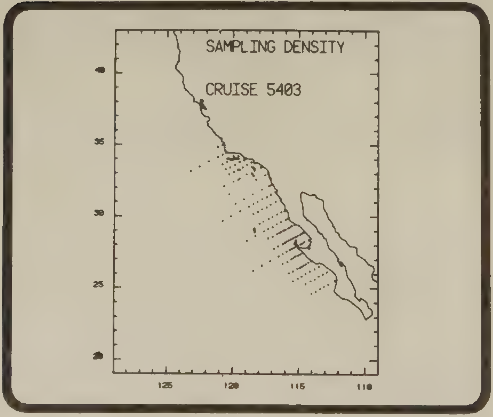
```
                      CalCOFI Cruises
        Begin    End           # of    Min    Max     Min   Max
Cruise  Date     Date   Ship Stations    Lines         Stations

 5401   540107  540120   CR      59  113.0  150.0    19.0 140.0
 5401   540105  540122   HO      75   77.0  110.0    27.0 110.0
 5402   540203  540213   CR      51   77.0  100.0    27.0  80.0
 5402   540204  540215   HO      85  103.0  137.0    23.0  80.0
 5403   540305  540312   CR      38   77.0   93.0    27.0  90.0
 5403   540304  540318   HO     115   97.0  137.0    23.0  90.0
 5404   540408  540417   CR      66  117.0  137.0    23.0  70.0
 5404   540409  540420   ES      50   93.0  107.0    27.0 100.0
 5404   540407  540430   HO      80   60.0  113.0    28.0  90.0
 5405   540509  540524   CR      84   60.0   97.0    27.0  90.0
 5405   540506  540521   HO     121  100.0  137.0    23.0 100.0
 5406   540604  540622   CR     125   97.0  137.0    23.0  90.0
 5406   540604  540620   HO      84   50.0   93.0    27.0 100.0
 5407   540709  540721   CR      61   60.0   97.0    27.0 100.0
 5407   540708  540718   HO      57  100.0  137.0    23.0  90.0
 5408   540821  540901   CR      56  100.0  137.0    23.0  90.0
 5408   540827  540909   SB      66   60.0   97.0    27.0 100.0
 5410   541006  541017   CR      56   77.0  100.0    27.0  90.0

   Press <RETURN> for more or 0 to abort listing:
```

**1.2. GEOGRAPHIC SAMPLING DENSITY BY CRUISE** option provides a list of all stations occupied, the type of plankton tow(s) conducted at each station and whether a hydrocast was obtained. The researcher is asked to specify the cruise. Cruise numbers are four-digit codes; the first two designate the year and the last two designate the month. Typical screen output:



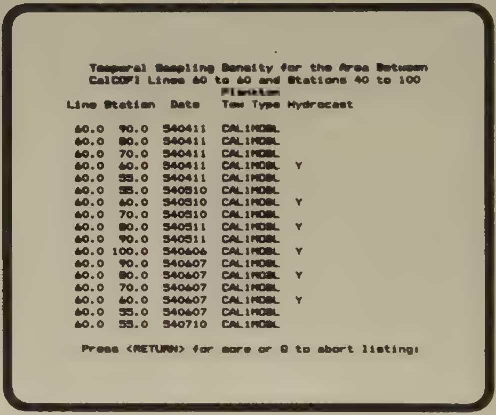
```
     Geographic Sampling Density for Cruise 5403
                      Plankton
  Line Station Tow Type Hydrocast

   87.0   35.0   CAL1MOBL
   87.0   40.0   CAL1MOBL   Y
   87.0   45.0   CAL1MOBL
   87.0   50.0   CAL1MOBL   Y
   87.0   55.0   CAL1MOBL
   87.0   60.0   CAL1MOBL   Y
   85.0   60.0   CAL1MOBL
   85.0   55.0   CAL1MOBL   Y
   85.0   50.0   CAL1MOBL
   85.0   45.0   CAL1MOBL   Y
   85.0   40.0   CAL1MOBL
   85.0   37.0   CAL1MOBL   Y
   83.0   40.0   CAL1MOBL
   83.0   43.0   CAL1MOBL   Y
   82.0   47.0   CAL1MOBL   Y
   83.0   48.0   CAL1MOBL
   83.0   51.0   CAL1MOBL   Y
   83.0   55.0   CAL1MOBL

    Press <RETURN> for more or Q to abort listing:
```

Those who are connected by graphic terminals can select the plot option. Typical screen output:



Press <RETURN> to clear plot from screen and return to **STATION INDEX MENU**.

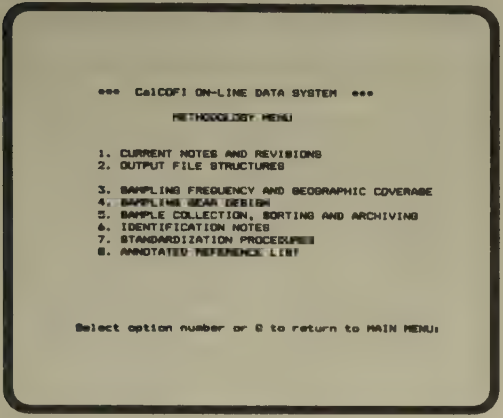
**1.3. TEMPORAL SAMPLING DENSITY BY AREA** option provides a list of all stations ever occupied, the dates, the type of plankton tow(s) conducted and whether a hydrocast was obtained for the geographic area and the years specified by the researcher. Areas are specified by the northernmost and southernmost line number and by the inshore and offshore station number; consult the station grid on the first page of this manual when specifying areas. Typical screen output:



```
     Temporal Sampling Density for the Area Between
     CalCOFI Lines 60 to 60 and Stations 40 to 100
                          Plankton
  Line Station  Date    Tow Type Hydrocast

   60.0   90.0  540411   CAL1MOBL
   60.0   80.0  540411   CAL1MOBL
   60.0   70.0  540411   CAL1MOBL
   60.0   60.0  540411   CAL1MOBL   Y
   60.0   55.0  540411   CAL1MOBL
   60.0   55.0  540510   CAL1MOBL
   60.0   60.0  540510   CAL1MOBL   Y
   60.0   70.0  540510   CAL1MOBL
   60.0   80.0  540511   CAL1MOBL   Y
   60.0   90.0  540511   CAL1MOBL
   60.0  100.0  540606   CAL1MOBL   Y
   60.0   90.0  540607   CAL1MOBL
   60.0   80.0  540607   CAL1MOBL   Y
   60.0   70.0  540607   CAL1MOBL
   60.0   60.0  540607   CAL1MOBL   Y
   60.0   55.0  540607   CAL1MOBL
   60.0   55.0  540710   CAL1MOBL

    Press <RETURN> for more or Q to abort listing:
```

## 2. METHODOLOGY

Each of the Methodology options has an associated submenu to further refine a request for information. Text is displayed on the terminal screen. Any portion of the text can be written to a computer file for subsequent printing.



```
***  CalCOFI ON-LINE DATA SYSTEM  ***

          METHODOLOGY MENU


1. CURRENT NOTES AND REVISIONS
2. OUTPUT FILE STRUCTURES

3. SAMPLING FREQUENCY AND GEOGRAPHIC COVERAGE
4. SAMPLING GEAR DESIGN
5. SAMPLE COLLECTION, SORTING AND ARCHIVING
6. IDENTIFICATION NOTES
7. STANDARDIZATION PROCEDURES
8. ANNOTATED REFERENCE LIST




Select option number or 0 to return to MAIN MENU:
```

**2.1. CURRENT NOTES AND REVISIONS** option provides access to the latest programmer's notes, a description of the data currently available, and computer charges for typical sessions.

**2.2. OUTPUT FILE STRUCTURES** option describes the output data file formats for the eleven file types available.

**2.3. SAMPLING FREQUENCY AND GEOGRAPHIC COVERAGE** option describes the cruise frequency and geographic coverage for four eras: 1951-60, 1961-65, 1966-84, 1985-87.

**2.4. SAMPLING GEAR DESIGN** option describes the CAL1MOBL, CALBOBL, and CALVET plankton samplers and their deployment.

**2.5. SAMPLE COLLECTION, SORTING AND ARCHIVING** option describes field collection methods, sorting procedures, larval length categories, and anchovy egg stages.

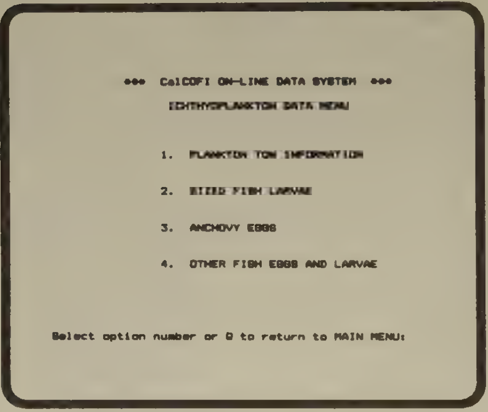
**2.6. IDENTIFICATION NOTES** option describes the number of taxonomic categories used during four eras: 1950's, 1960's, 1970's and 1980's.

**2.7. STANDARDIZATION PROCEDURES** option describes the adjustment for fractional sorting and the standard haul factor.

**2.8. ANNOTATED REFERENCE LIST** option lists sampling manuals, data reports and atlases, and references on estimates of egg and larval mortality and spawning biomass.

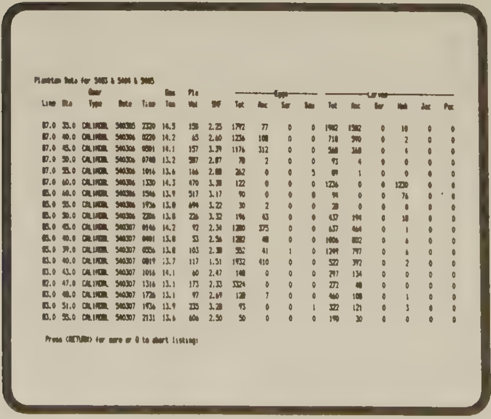
## 3. ICHTHYOPLANKTON DATA

Ichthyoplankton Data extracts data from the files created from analyses of the CalCOFI plankton samples. The researcher is asked to specify the cruise(s) and, for some options, the fish species of interest.

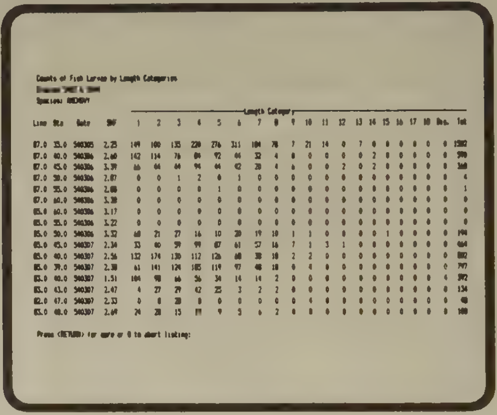


```
*** CalCOFI ON-LINE DATA SYSTEM ***
ICHTHYOPLANKTON DATA MENU

1. PLANKTON TOW INFORMATION

2. SIZED FISH LARVAE

3. ANCHOVY EGGS

4. OTHER FISH EGGS AND LARVAE

Select option number or 0 to return to MAIN MENU:
```

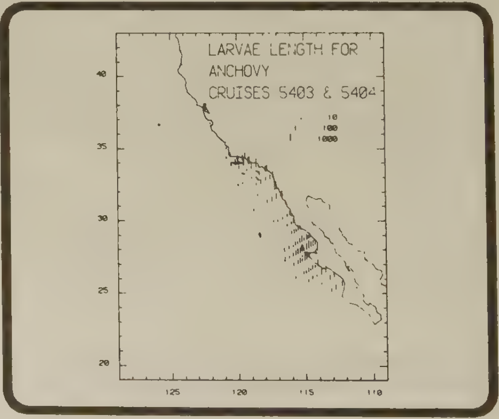
**3.1. PLANKTON TOW INFORMATION** option lists gear type, date and time of tow, plankton volume, sea surface temperature, standard haul factor, total number of fish eggs, numbers of anchovy, sardine and saury eggs, total number of fish larvae, and numbers of anchovy, sardine, saury, hake, jack mackerel and Pacific mackerel larvae for each station occupied during the cruise(s) specified. Typical screen output (132-column format):



**3.2. SIZED FISH LARVAE** option provides counts of fish larvae by length categories. Category definitions can be found under the "Methodology" option of the main menu. The researcher is asked to specify the cruise(s) and species (anchovy, sardine, hake, jack mackerel, or Pacific mackerel) of interest. Typical screen output (132-column format):

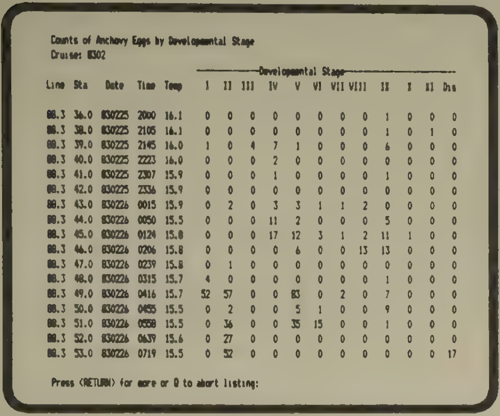


Those who are connected by graphics terminals can display plots of selected length categories of larvae for selected species. Typical screen output:



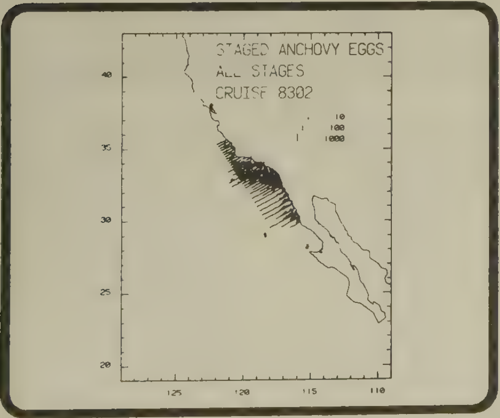
Press <RETURN> to clear plot from screen and return to **ICHTHYOPLANKTON DATA MENU.**

**3.3. ANCHOVY EGGS** option provides counts of anchovy eggs by developmental stage; the time of the tow and the water temperature are also listed. Stage definitions can be found under the MAIN MENU "Methodology" option. The researcher is asked to specify the cruise(s) of interest. These data are available only from the CalVET samples obtained for the anchovy biomass surveys (1980-85). Typical screen output (132-column format):



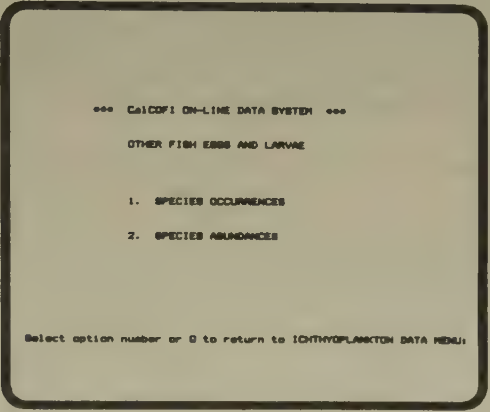
```
Counts of Anchovy Eggs by Developmental Stage
Cruise: 8302
                                  ------------Developmental Stage----------------------------
Line  Sta   Date    Time  Temp     I   II  III   IV    V   VI  VII VIII   IX    X   XI  Dis

88.3  36.0  830225  2000  16.1     0    0    0    0    0    0    0    0    1    0    0    0
88.3  38.0  830225  2105  16.1     0    0    0    0    0    0    0    0    1    0    1    0
88.3  39.0  830225  2145  16.0     1    0    4    7    1    0    0    0    6    0    0    0
88.3  40.0  830225  2223  16.0     0    0    0    2    0    0    0    0    0    0    0    0
88.3  41.0  830225  2307  15.9     0    0    0    1    0    0    0    0    1    0    0    0
88.3  42.0  830225  2336  15.9     0    0    0    0    0    0    0    0    0    0    0    0
88.3  43.0  830226  0015  15.9     0    2    0    3    3    1    1    2    0    0    0    0
88.3  44.0  830226  0050  15.5     0    0    0   11    2    0    0    0    5    0    0    0
88.3  45.0  830226  0124  15.8     0    0    0   17   12    3    1    2   11    1    0    0
88.3  46.0  830226  0206  15.8     0    0    0    0    6    0    0   13   13    0    0    0
88.3  47.0  830226  0239  15.8     0    1    0    0    0    0    0    0    0    0    0    0
88.3  48.0  830226  0315  15.7     4    0    0    0    0    0    0    0    1    0    0    0
88.3  49.0  830226  0416  15.7    52   57    0    0   83    0    2    0    7    0    0    0
88.3  50.0  830226  0455  15.5     0    2    0    0    5    1    0    0    9    0    0    0
88.3  51.0  830226  0558  15.5     0   36    0    0   35   15    0    0    1    0    0    0
88.3  52.0  830226  0639  15.6     0   27    0    0    0    0    0    0    0    0    0    0
88.3  53.0  830226  0719  15.5     0   52    0    0    0    0    0    0    0    0    0   17

Press <RETURN> for more or 0 to abort listing:
```

Those who are connected by graphics terminals can display plots of selected stages of eggs. Typical screen output:



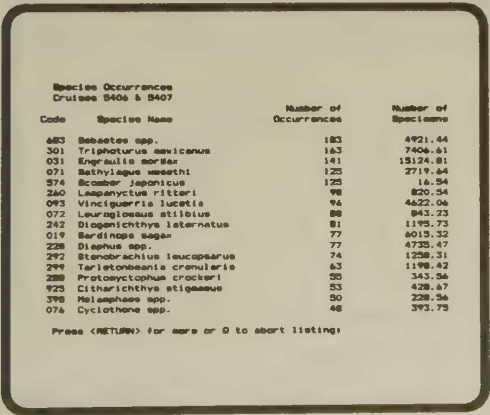
Press <RETURN> to clear plot from screen and return to **ICHTHYOPLANKTON DATA MENU.**

**3.4. OTHER FISH EGGS AND LARVAE** option will display a submenu:



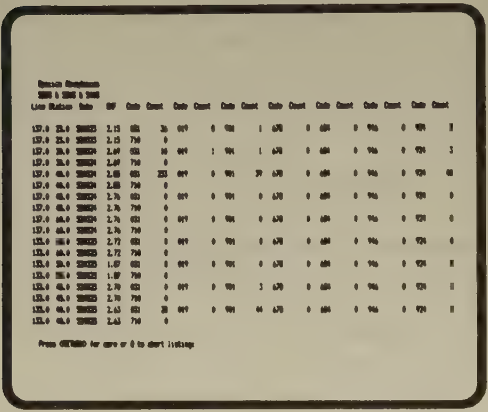
```
          *** CalCOFI ON-LINE DATA SYSTEM ***

              OTHER FISH EGGS AND LARVAE


              1.  SPECIES OCCURRENCES

              2.  SPECIES ABUNDANCES



Select option number or 0 to return to ICHTHYOPLANKTON DATA MENU:
```

3.4.1. SPECIES OCCURRENCES option provides a list of taxonomic categories, the number of occurrences of each, and standardized counts of each for the cruise(s) specified by the researcher. Typical screen output:

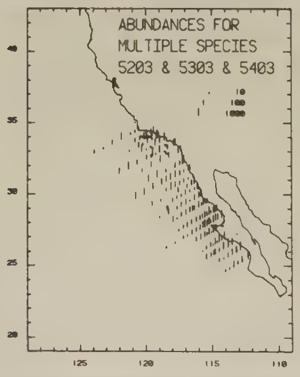


```
  Species Occurrences
  Cruises 8406 & 8407
                                         Number of        Number of
Code     Species Name                   Occurrences       Specimens

 683  Sebastes spp.                             183         4921.44
 301  Triphoturus mexicanus                     163         7404.61
 031  Engraulis mordax                          141        15124.81
 071  Bathylagus wesethi                        125         2719.64
 574  Scomber japonicus                         123           16.54
 260  Lampanyctus ritteri                        98          820.54
 093  Vinciguerria lucetia                       96         4622.06
 072  Leuroglossus stilbius                      88          843.23
 242  Diogenichthys laternatus                   81         1195.73
 019  Sardinops sagax                            77         6015.32
 228  Diaphus spp.                               77         4733.47
 292  Stenobrachius leucopsarus                  74         1258.31
 299  Tarletonbeania crenularis                  63         1198.42
 288  Protomyctophum crockeri                    55          343.56
 925  Citharichthys stigmaeus                    53          428.67
 398  Melamphaes spp.                            50          228.56
 076  Cyclothone spp.                            48          393.75

  Press <RETURN> for more or 0 to abort listing:
```

3.4.2. SPECIES ABUNDANCES option provides specimen counts for each station occupied. The researcher is asked for the cruise(s) and taxon of interest. Consult the code list at the end of this manual when specifying desired taxonomic categories. The researcher may elect to display only positive stations, however, the computer file contains both positive and negative stations. Typical screen output (132 column format):



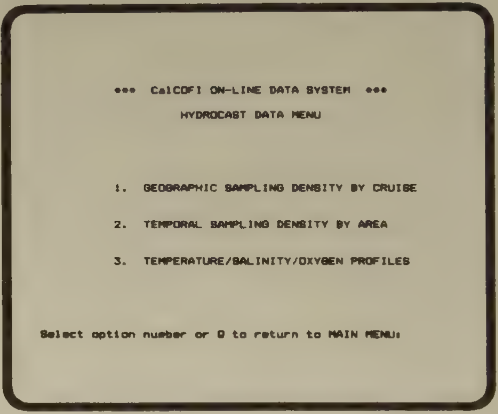
Those who are connected by graphics terminals can display a plot of the total number of specimens in the selected taxonomic categories. Typical screen output:



Press <RETURN> to clear plot from screen and return to **OTHER FISH EGGS AND LARVAE MENU.**

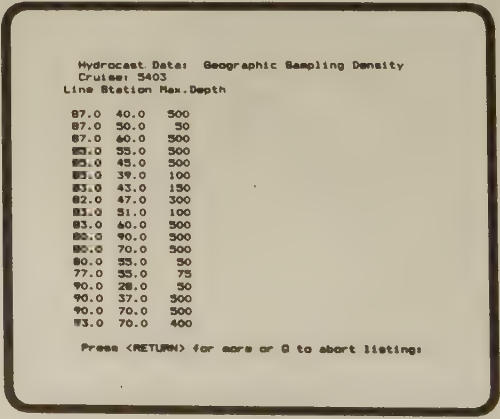
## 4. HYDROCAST DATA

Hydrocast Data provides access to data files created from analyses of water samples. These data files, originally processed by Scripps Institution of Oceanography, contain measurements of temperature, salinity and oxygen content at standard depths. The first two options allow the researcher to explore the extent of the hydrocast data; the last option is used to extract desired data.



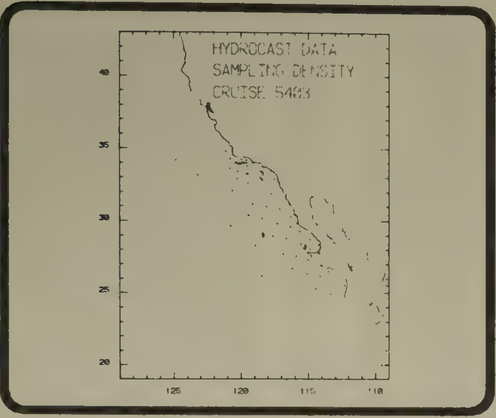
```
*** CalCOFI ON-LINE DATA SYSTEM ***

        HYDROCAST DATA MENU


1.  GEOGRAPHIC SAMPLING DENSITY BY CRUISE

2.  TEMPORAL SAMPLING DENSITY BY AREA

3.  TEMPERATURE/SALINITY/OXYGEN PROFILES


Select option number or 0 to return to MAIN MENU:
```

**4.1. GEOGRAPHIC SAMPLING DENSITY BY CRUISE** option provides a list of hydrocasts, the equipment used and the maximum depth sampled. The researcher is asked to specify the cruise of interest. Typical screen output:



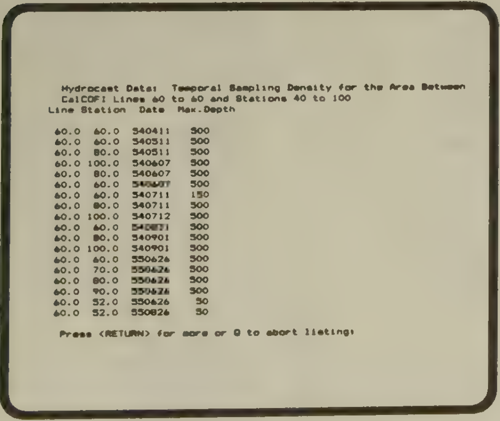
```
  Hydrocast Data:  Geographic Sampling Density
  Cruise: 5403
Line Station Max.Depth

 87.0  40.0   500
 87.0  50.0    50
 87.0  60.0   500
 [illegible].0  55.0   500
 [illegible].0  45.0   500
 [illegible].0  39.0   100
 [illegible].0  43.0   150
 82.0  47.0   300
 [illegible].0  51.0   100
 83.0  60.0   500
 [illegible].0  90.0   500
 [illegible].0  70.0   500
 80.0  55.0    50
 77.0  55.0    75
 90.0  28.0    50
 90.0  37.0   500
 90.0  70.0   500
 [illegible]3.0  70.0   400

 Press <RETURN> for more or 0 to abort listing:
```

Those who are connected by graphic terminals can select the plot option. Typical screen output:



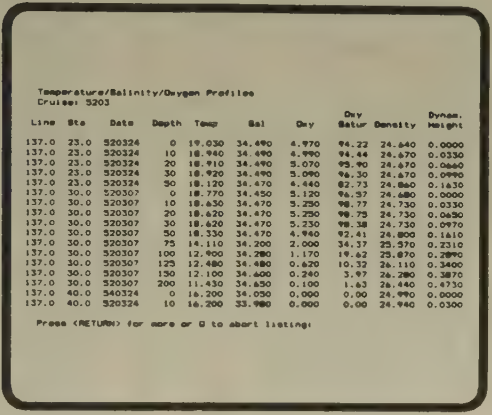
Press <RETURN> to clear plot from screen and return to **HYDROCAST DATA MENU**.

**4.2. TEMPORAL SAMPLING DENSITY BY AREA** option provides a list of station locations, dates, equipment used, and maximum depth sampled. The researcher is asked to specify the geographic area and year(s) of interest.



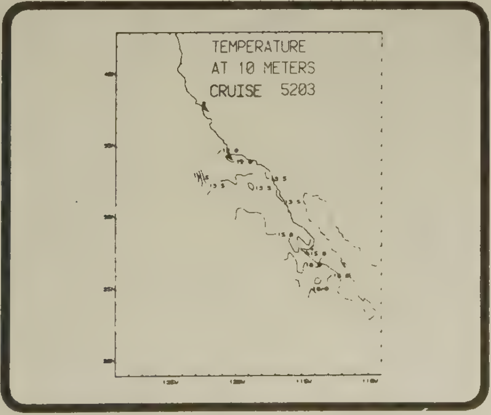
```
  Hydrocast Data:  Temporal Sampling Density for the Area Between
  CalCOFI Lines 60 to 60 and Stations 40 to 100
Line Station  Date  Max.Depth

 60.0   60.0  540411    500
 60.0   60.0  540511    500
 60.0   80.0  540511    500
 60.0 100.0  540607    500
 60.0   80.0  540607    500
 60.0   60.0  540607    500
 60.0   60.0  540711    150
 60.0   80.0  540711    500
 60.0 100.0  540712    500
 60.0   60.0  540821    500
 60.0   80.0  540901    500
 60.0 100.0  540901    500
 60.0   60.0  550626    500
 60.0   70.0  550626    500
 60.0   80.0  550626    500
 60.0   90.0  550626    500
 60.0   52.0  550626     50
 60.0   52.0  550826     50

  Press <RETURN> for more or Q to abort listing:
```

**4.3. TEMPERATURE/SALINITY/OXYGEN PROFILES** option lists the temperature, salinity, oxygen content, oxygen saturation, density, and dynamic height anomaly at standard depths for each hydrocast. Researcher is asked to specify the cruise(s) of interest. Typical screen output:



```
  Temperature/Salinity/Oxygen Profiles
  Cruise: 5203
                                                           Oxy            Dynam.
 Line   Sta    Date    Depth  Temp     Sal      Oxy      Satur Density  Height

 137.0  23.0  520324      0  19.030  34.490   4.970     94.22  24.640  0.0000
 137.0  23.0  520324     10  18.940  34.490   4.990     94.44  24.670  0.0330
 137.0  23.0  520324     20  18.910  34.490   5.070     95.90  24.670  0.0660
 137.0  23.0  520324     30  18.920  34.490   5.090     96.30  24.670  0.0990
 137.0  23.0  520324     50  18.120  34.470   4.440     82.73  24.860  0.1630
 137.0  30.0  520307      0  18.770  34.450   5.120     96.57  24.680  0.0000
 137.0  30.0  520307     10  18.630  34.470   5.250     98.77  24.730  0.0330
 137.0  30.0  520307     20  18.620  34.470   5.250     98.75  24.730  0.0650
 137.0  30.0  520307     30  18.620  34.470   5.230     98.38  24.730  0.0970
 137.0  30.0  520307     50  18.330  34.470   4.940     92.41  24.800  0.1610
 137.0  30.0  520307     75  14.110  34.200   2.000     34.37  25.570  0.2310
 137.0  30.0  520307    100  12.900  34.280   1.170     19.62  25.870  0.2890
 137.0  30.0  520307    125  12.480  34.480   0.620     10.32  26.110  0.3400
 137.0  30.0  520307    150  12.100  34.600   0.240      3.97  26.280  0.3870
 137.0  30.0  520307    200  11.430  34.650   0.100      1.63  26.440  0.4730
 137.0  40.0  540324      0  16.200  34.050   0.000      0.00  24.990  0.0000
 137.0  40.0  520324     10  16.200  33.980   0.000      0.00  24.940  0.0300

  Press <RETURN> for more or Q to abort listing:
```

Those who are connected by a graphics terminal can display isopleth plots of the variables at a standard depth. Researcher is asked to specify the variable and depth of interest. Typical screen output:



# TAXONOMIC CODES

## Specimens which could not be identified to species were assigned to the larger taxonomic categories of genera, families, or orders

### ELOPIFORMES

| | |
|---|---|
| 005 | Albulidae |
| 006 | Albula spp. |
| 007 | Albula vulpes |
| 003 | Elopidae |
| 004 | Elops affinis |

### ANGUILLIFORMES

| | |
|---|---|
| 355 | Anguilliformes |
| 358 | Congridae |
| 359 | Ariosoma spp. |
| 360 | Hildebrandia spp. |
| 368 | Cyematidae |
| 370 | Muraenidae |
| 375 | Ophichthidae |
| 378 | Serrivomeridae |

### CLUPEIFORMES

| | |
|---|---|
| 015 | Clupeidae |
| 011 | Etrumeus spp. |
| 012 | Etrumeus acuminatus |
| 016 | Opisthonema spp. |
| 019 | Sardinops sagax |
| 025 | Engraulidae |
| 026 | Anchoa spp. |
| 031 | Engraulis mordax |

### SALMONIFORMES

| | |
|---|---|
| 108 | Salmoniformes |
| 035 | Alepocephalidae |
| 036 | Alepocephalus spp. |
| 055 | Argentinidae |
| 056 | Argentina sialis |
| 058 | Microstoma microstoma |
| 061 | Nansenia spp. |
| 062 | Nansenia candida |
| 063 | Nansenia crassa |
| 065 | Bathylagidae |
| 070 | Bathylagus spp. |
| 073 | Bathylagus longirostris |
| 066 | Bathylagus milleri |
| 067 | Bathylagus nigrigenys |
| 068 | Bathylagus ochotensis |
| 069 | Bathylagus pacificus |
| 071 | Bathylagus wesethi |
| 074 | Leuroglossus schmidti |
| 072 | Leuroglossus stilbius |
| 050 | Opisthoproctidae |
| 054 | Bathylychnops exilis |
| 051 | Dolichopteryx spp. |
| 052 | Dolichopteryx longipes |
| 053 | Macropinna microstoma |
| 045 | Osmeridae |

### STOMIIFORMES

| | |
|---|---|
| 109 | Stomiiformes |
| 075 | Gonostomatidae |
| 076 | Cyclothone spp. |
| 077 | Cyclothone acclinidens |
| 078 | Cyclothone signata |
| 084 | Danaphos oculatus |
| 086 | Diplophos spp. |
| 087 | Diplophos taenia |
| 080 | Gonostoma spp. |
| 088 | Ichthyococcus spp. |
| 089 | Ichthyococcus irregularis |
| 091 | Valenciennellus stellatus |
| 092 | Vinciguerria spp. |
| 093 | Vinciguerria lucetia |
| 094 | Vinciguerria poweriae |
| 095 | Woodsia nonsuchae |
| 100 | Sternoptychidae |
| 101 | Argyropelecus spp. |
| 103 | Argyropelecus affinis |
| 102 | Argyropelecus lychnus |
| 105 | Argyropelecus sladeni |
| 107 | Sternoptyx spp. |
| 110 | Astronesthidae |
| 155 | Chauliodontidae |
| 156 | Chauliodus macouni |
| 160 | Idiacanthidae |
| 161 | Idiacanthus antrostomus |
| 150 | Malacosteidae |
| 151 | Aristostomias scintillans |
| 130 | Melanostomiidae |
| 131 | Bathophilus spp. |
| 132 | Bathophilus filifer |
| 133 | Bathophilus flemingi |
| 136 | Eustomias spp. |
| 137 | Leptostomias spp. |
| 139 | Photonectes spp. |
| 142 | Tactostoma macropus |
| 120 | Stomiidae |
| 121 | Stomias atriventer |

### MYCTOPHIFORMES

| | |
|---|---|
| 190 | Myctophiformes |
| 210 | Alepisauridae |
| 211 | Alepisaurus ferox |
| 326 | Anotopterus pharao |
| 345 | Evermannellidae |
| 346 | Evermannella indica |
| 330 | Omosudidae |
| 331 | Omosudis lowei |
| 310 | Paralepididae |
| 312 | Lestidiops spp. |
| 311 | Lestidiops ringens |
| 317 | Notolepis risso |
| 318 | Paralepis atlantica |
| 314 | Stemonosudis spp. |
| 315 | Stemonosudis macrura |
| 321 | Sudis atrox |
| 200 | Aulopidae |
| 201 | Aulopus spp. |
| 195 | Notosudidae |
| 196 | Scopelosaurus spp. |
| 335 | Scopelarchidae |
| 334 | Benthalbella spp. |
| 336 | Benthalbella dentata |
| 337 | Benthalbella linguidens |
| 343 | Rosenblattichthys volucris |
| 342 | Scopelarchoides nicholsi |
| 338 | Scopelarchus spp. |
| 339 | Scopelarchus analis |
| 340 | Scopelarchus guentheri |
| 341 | Scopelarchus stephensi |
| 215 | Myctophidae |
| 216 | Disintegrated myctophid |
| 255 | Bolinichthys spp. |
| 225 | Ceratoscopelus spp. |
| 226 | Ceratoscopelus townsendi |
| 228 | Diaphus spp. |
| 229 | Diaphus pacificus |
| 227 | Diaphus theta |
| 257 | Lampadena spp. |
| 256 | Lampadena urophaos |
| 261 | Lampanyctus spp. |
| 262 | Lampanyctus idostigma |
| 263 | Lampanyctus omostigma |
| 264 | Lampanyctus parvicauda |
| 259 | Lampanyctus regalis |
| 260 | Lampanyctus ritteri |
| 266 | Lobianchia spp. |
| 281 | Notolychnus valdiviae |
| 283 | Notoscopelus resplendens |
| 286 | Parvilux ingens |
| 292 | Stenobrachius leucopsarus |
| 258 | Taaningichthys minimus |
| 303 | Triphoturus spp. |
| 301 | Triphoturus mexicanus |
| 302 | Triphoturus nigrescens |
| 217 | Benthosema pterota |
| 219 | Benthosema suborbitale |
| 221 | Centrobranchus spp. |
| 241 | Diogenichthys spp. |
| 239 | Diogenichthys atlanticus |
| 242 | Diogenichthys laternatus |
| 243 | Electrona rissoi |
| 249 | Gonichthys tenuiculus |
| 250 | Hygophum spp. |
| 251 | Hygophum atratum |
| 253 | Hygophum proximum |
| 252 | Hygophum reinhardtii |
| 270 | Loweina rara |
| 274 | Myctophum spp. |
| 272 | Myctophum aurolaternatum |
| 275 | Myctophum lychnobium |
| 273 | Myctophum nitidulum |
| 289 | Protomyctophum spp. |
| 288 | Protomyctophum crockeri |
| 287 | Protomyctophum thompsoni |
| 296 | Symbolophorus californiensis |
| 297 | Symbolophorus evermanni |
| 299 | Tarletonbeania crenularis |
| 204 | Synodontidae |
| 206 | Synodus spp. |
| 207 | Synodus lucioceps |

### GADIFORMES

| | |
|---|---|
| 885 | Bregmacerotidae |
| 886 | Bregmaceros spp. |
| 887 | Bregmaceros bathymaster |
| 905 | Gadidae |
| 904 | Gadus macrocephalus |
| 906 | Microgadus proximus |
| 907 | Theragra chalcogramma |
| 900 | Merlucciidae |
| 901 | Merluccius productus |
| 909 | Moridae |
| 908 | Physiculus spp. |
| 895 | Macrouridae |
| 891 | Coryphaenoides spp. |

### OPHIDIIFORMES

| | |
|---|---|
| 869 | Ophidiiformes |
| 865 | Bythitidae |
| 866 | Brosmophycis marginata |
| 875 | Carapidae |
| 870 | Ophidiidae |
| 872 | Chilara taylori |
| 871 | Ophidion scrippsae |

### BATRACOIDIFORMES

| | |
|---|---|
| 820 | Batrachoididae |
| 821 | Porichthys spp. |

### LOPHIIFORMES

| | |
|---|---|
| 971 | Lophiiformes |
| 960 | Antennariidae |
| 961 | Antennarius spp. |
| 985 | Chaunacidae |
| 986 | Chaunax spp. |
| 996 | Ogcocephalidae |
| 990 | Ceratioidei |
| 992 | Ceratiidae |
| 995 | Gigantactinidae |
| 993 | Linophrynidae |
| 994 | Melanocetidae |
| 991 | Oneirodidae |
| 975 | Lophiidae |

### GOBIESOCIFORMES

| | |
|---|---|
| 830 | Callionymidae |
| 825 | Gobiesocidae |

### BELONIFORMES

| | |
|---|---|
| 175 | Belonidae |
| 176 | Ablennes hians |
| 180 | Exocoetidae |
| 170 | Hemiramphidae |
| 181 | Oxyporhamphus micropterus |
| 165 | Scomberesocidae |
| 166 | Cololabis saira |

### ATHERINIFORMES

| | |
|---|---|
| 470 | Atherinidae |
| 471 | Atherinops spp. |

### LAMPRIDIFORMES

| | |
|---|---|
| 387 | Lophotidae |
| 380 | Trachipteridae |
| 385 | Desmodema spp. |
| 381 | Trachipterus spp. |
| 382 | Trachipterus altivelis |
| 383 | Trachipterus fukuzakii |
| 384 | Zu cristatus |
| 350 | Eutaeniophoridae |
| 351 | Eutaeniophorus spp. |

## BERYCIFORMES

| | |
|---|---|
| 388 | Beryciformes |
| 390 | Diretmidae |
| 391 | Diretmus pauciradiatus |
| 413 | Holocentridae |
| 395 | Melamphaidae |
| 398 | Melamphaes spp. |
| 396 | Melamphaes lugubris |
| 397 | Melamphaes parvus |
| 404 | Poromitra spp. |
| 409 | Scopeloberyx robustus |
| 412 | Scopelogadus bispinosus |

## SYNGNATHIFORMES

| | |
|---|---|
| 785 | Fistulariidae |
| 780 | Macroramphosidae |
| 781 | Macroramphosus gracilis |
| 790 | Syngnathidae |
| 791 | Syngnathus spp. |

## SCORPAENIFORMES

| | |
|---|---|
| 760 | Agonidae |
| 710 | Anoplopomatidae |
| 711 | Anoplopoma fimbria |
| 735 | Cottidae |
| 736 | Scorpaenichthys marmoratus |
| 770 | Cyclopteridae |
| 715 | Hexagrammidae |
| 717 | Hexagrammos spp. |
| 721 | Ophiodon spp. |
| 720 | Ophiodon elongatus |
| 730 | Oxylebius pictus |
| 726 | Zaniolepis spp. |
| 670 | Scorpaenidae |
| 671 | Pontinus spp. |
| 676 | Scorpaena spp. |
| 678 | Scorpaena guttata |
| 675 | Scorpaenodes xyris |
| 683 | Sebastes spp. |
| 688 | Sebastes aurora |
| 684 | Sebastes jordani |
| 685 | Sebastes levis |
| 687 | Sebastes macdonaldi |
| 686 | Sebastes paucispinis |
| 707 | Sebastolobus spp. |
| 708 | Sebastolobus alascanus |
| 709 | Sebastolobus altivelis |
| 755 | Triglidae |
| 756 | Prionotus spp. |

## PERCIFORMES

| | |
|---|---|
| 423 | Perciformes |
| 585 | Acanthuridae |
| 880 | Ammodytidae |
| 881 | Ammodytes hexapturus |
| 845 | Blennioidei |
| 855 | Bathymasteridae |
| 850 | Blenniidae |
| 851 | Hypsoblennius spp. |
| 840 | Clinidae |
| 841 | Gibbonsia spp. |
| 848 | Pholididae |
| 846 | Stichaeidae |
| 795 | Gobiidae |
| 798 | Coryphopterus nicholsii |
| 844 | Microdesmidae |
| 540 | Icosteidae |
| 541 | Icosteus aenigmaticus |
| 635 | Labridae |
| 636 | Halichoeres spp. |
| 639 | Oxyjulis californica |
| 641 | Semicossyphus pulcher |
| 625 | Pomacentridae |
| 626 | Chromis punctipinnis |
| 627 | Hypsypops rubicundus |
| 650 | Scaridae |
| 480 | Mugilidae |
| 481 | Mugil spp. |
| 445 | Apogonidae |
| 446 | Howella brodiei |
| 550 | Bramidae |
| 551 | Brama spp. |
| 552 | Brama japonica |
| 500 | Carangidae |
| 501 | Caranx spp. |
| 506 | Chloroscombrus orqueta |
| 509 | Decapterus scombrinus |
| 512 | Naucrates ductor |
| 513 | Oligoplites spp. |
| 516 | Seriola spp. |
| 517 | Seriola lalandi |
| 514 | Trachurus symmetricus |
| 558 | Caristiidae |
| 559 | Caristius macropus |
| 555 | Coryphaenidae |
| 554 | Coryphaena spp. |
| 557 | Coryphaena equisetis |
| 556 | Coryphaena hippurus |
| 615 | Ephippidae |
| 616 | Chaetodipterus zonatus |
| 495 | Gerreidae |
| 496 | Eucinostomus spp. |
| 600 | Haemulidae |
| 601 | Anisotremus davidsoni |
| 451 | Xenichthys xanti |
| 452 | Xenistius californiensis |
| 660 | Kyphosidae |
| 656 | Girella nigricans |
| 664 | Hermosilla azurea |
| 661 | Kyphosus spp. |
| 666 | Medialuna californiensis |
| 450 | Lutjanidae |
| 810 | Malacanthidae |
| 811 | Caulolatilus princeps |
| 460 | Mullidae |
| 440 | Priacanthidae |
| 610 | Sciaenidae |
| 609 | Atractoscion nobilis |
| 614 | Cheilotrema saturnum |
| 611 | Cynoscion spp. |
| 612 | Genyonemus lineatus |
| 617 | Menticirrhus spp. |
| 618 | Roncador stearnsii |
| 613 | Seriphus politus |
| 619 | Umbrina roncador |
| 425 | Serranidae |
| 435 | Anthiinae |
| 427 | Epinephelinae |
| 426 | Epinephelus spp. |
| 438 | Grammistinae |
| 430 | Serraninae |
| 431 | Paralabrax spp. |
| 605 | Sparidae |
| 607 | Calamus brachysomus |
| 490 | Polynemidae |
| 590 | Gempylidae |
| 597 | Diplospinus multistriatus |
| 591 | Gempylus serpens |
| 592 | Nealotus tripes |
| 560 | Scombridae |
| 561 | Auxis spp. |
| 564 | Euthynnus spp. |
| 567 | Katsuwonus pelamis |
| 571 | Sarda chiliensis |
| 574 | Scomber japonicus |
| 577 | Scomberomorus spp. |
| 581 | Thunnus albacares |
| 595 | Trichiuridae |
| 596 | Lepidopus xantusi |
| 598 | Trichiurus nitens |
| 485 | Sphyraenidae |
| 486 | Sphyraena argentea |
| 535 | Centrolophidae |
| 536 | Icichthys lockingtoni |
| 520 | Nomeidae |
| 522 | Cubiceps spp. |
| 526 | Cubiceps caeruleus |
| 527 | Cubiceps pauciradiatus |
| 521 | Nomeus gronovii |
| 523 | Psenes spp. |
| 525 | Psenes pellucidus |
| 524 | Psenes sio |
| 530 | Stromateidae |
| 532 | Peprilus spp. |
| 531 | Peprilus simillimus |
| 545 | Tetragonuridae |
| 547 | Tetragonurus atlanticus |
| 546 | Tetragonurus cuvieri |
| 815 | Chiasmodontidae |
| 816 | Chiasmodon niger |
| 835 | Uranoscopidae |
| 836 | Astroscopus spp. |
| 860 | Zoarcidae |

## PLEURONECTIFORMES

| | |
|---|---|
| 915 | Pleuronectiformes |
| 916 | Bothidae |
| 917 | Bothus spp. |
| 918 | Bothus leopardinus |
| 931 | Engyophrys sancti-laurentii |
| 937 | Monolene spp. |
| 924 | Citharichthys spp. |
| 921 | Citharichthys fragilis |
| 922 | Citharichthys gilberti |
| 920 | Citharichthys platophrys |
| 923 | Citharichthys sordidus |
| 925 | Citharichthys stigmaeus |
| 926 | Citharichthys xanthostigma |
| 930 | Cyclopsetta spp. |
| 928 | Etropus spp. |
| 933 | Hippoglossina spp. |
| 929 | Hippoglossina stomata |
| 934 | Paralichthys spp. |
| 932 | Paralichthys californicus |
| 927 | Syacium ovale |
| 936 | Xystreurys liolepis |
| 940 | Pleuronectidae |
| 959 | Atheresthes stomias |
| 961 | Embassichthys bathybius |
| 960 | Eopsetta jordani |
| 941 | Glyptocephalus zachirus |
| 947 | Hippoglossoides elassodon |
| 945 | Hippoglossus stenolepis |
| 942 | Hypsopsetta guttulata |
| 963 | Inopsetta ischyra |
| 962 | Isopsetta isolepis |
| 944 | Lepidopsetta bilineata |
| 943 | Lyopsetta exilis |
| 946 | Microstomus pacificus |
| 948 | Parophrys vetulus |
| 949 | Platichthys stellatus |
| 954 | Pleuronichthys spp. |
| 951 | Pleuronichthys coenosus |
| 952 | Pleuronichthys decurrens |
| 953 | Pleuronichthys ritteri |
| 955 | Pleuronichthys verticalis |
| 958 | Psettichthys melanostictus |
| 950 | Reinhardtius hippoglossoides |
| 965 | Cynoglossidae |
| 966 | Symphurus spp. |
| 968 | Soleidae |
| 969 | Achirus mazatlanus |

## TETRAODONTIFORMES

| | |
|---|---|
| 415 | Balistidae |
| 414 | Ostraciidae |
| 420 | Tetraodontidae |

| | |
|---|---|
| 002 | Disintegrated fish larva |
| 001 | Unidentified fish larva |

8806

## 5

# Seabird Relationships with Tropical Tunas and Dolphins

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Flocks of seabirds accompanying surface-schooling tunas are characteristic of tropical seas, but are especially notable in the eastern tropical Pacific (ETP) where the birds also associate with dolphins. We recently described these species interactions (Au and Pitman 1986) from extensive ship surveys that entailed the examination of cetacean schools, particularly those associated with birds and tuna. Our observations enabled us to form an ecological perspective of species behaviors and interrelationships. There have been few other studies on the oceanic ecology of ETP seabirds, although the birds are much watched by fishermen as indicators of fish and fishing conditions. King (1970, 1974a) and Gould (1971) presented the first comprehensive descriptions of tropical central and eastern Pacific birds at sea, but as their observations were primarily from ships conducting oceanographic surveys, they had limited opportunities for closeup observations of feeding flocks and were not able to study the relationships with cetaceans.

In this essay we review the relationships between seabirds, tuna, and cetaceans as observed in the ETP and describe the ecological role of tunas. We will explain how the organization of, and interactions within, the apex pelagic community might depend upon forage and foraging tactics, especially that of the tunas—perhaps the key top predators of tropical seas. Our inferences will be based largely upon the behavior of the birds and dolphins, as the tuna were seldom directly observable.

## Data and Methods

Observations on birds, tuna, and cetaceans were obtained from both biological census and oceanographic ship surveys. Most important were the Southwest Fisheries Center (SWFC) dolphin surveys of 1976, 1977, 1979, and 1980, designed to assess the distributions and abundances of dolphins involved in the "porpoise-tuna" fishery of the eastern Pacific. These surveys provided information over a broad area overlapping the tuna fishing grounds. In addition to our participation on these biological surveys, Pitman studied birds, tuna, and cetaceans from ships conducting physical oceanographic studies in the central and eastern Pacific.

The search and much of the observations were conducted through twenty or twenty-five power binoculars, generally mounted both port and starboard on or above the flying bridge of each survey ship. We usually searched between 6 A.M. and 6 P.M., using two teams of observers. The high powered binoculars proved indispensable for closeup observations and for minimizing the overlooking of bird flocks and cetacean schools. On the dolphin surveys, most mammal schools were approached closely after initial detection for better observations (often within a hundred meters), as were bird flocks if they appeared to be associated with cetaceans. Flocks and schools were usually not approached on the oceanographic surveys. On all surveys, species were identified whenever possible, and numbers estimated for all flocks and mammal schools. We took notes on any tuna seen, but direct observations or measurements of these fish schools were not feasible.

Noon positions from the above cruises, shown in figure 5.1, illustrate survey coverage. The concentrations of survey days along certain lines is due to repeated hydrographic transects on the oceanographic cruises. Though there were surveys during every month, about 63 percent of the observations took place during January through March; there is thus a seasonal bias in our data. A monthly breakdown of observations is given by Pitman (1986), and a more detailed description of the dolphin surveys by Au and Perryman (1985).

## Flock Characteristics

We defined a flock as an aggregate of ten or more birds. We did not include storm-petrels, phalaropes, tropic birds, or the occasional gulls, as they feed largely independently of fish schools in pelagic waters and rarely occur with either tuna or cetaceans. The 1977, 1979, and 1980 dolphin surveys provided the most representative and accurate subset of our observations; these data are summarized in table 5.1 (flock associations) and table 5.2 (flock composition) by 5° latitude intervals and according to eastern and western sectors. We sighted a total of 637 flocks in the eastern sector, and 125 flocks in the western sector (table 5.1). Overall, few (25 percent) of these flocks were with cetaceans, although the association rates were high in certain areas (see below). If we assume that flocks of ten or more birds are associated with tuna, most tuna schools, then, were not with cetaceans.

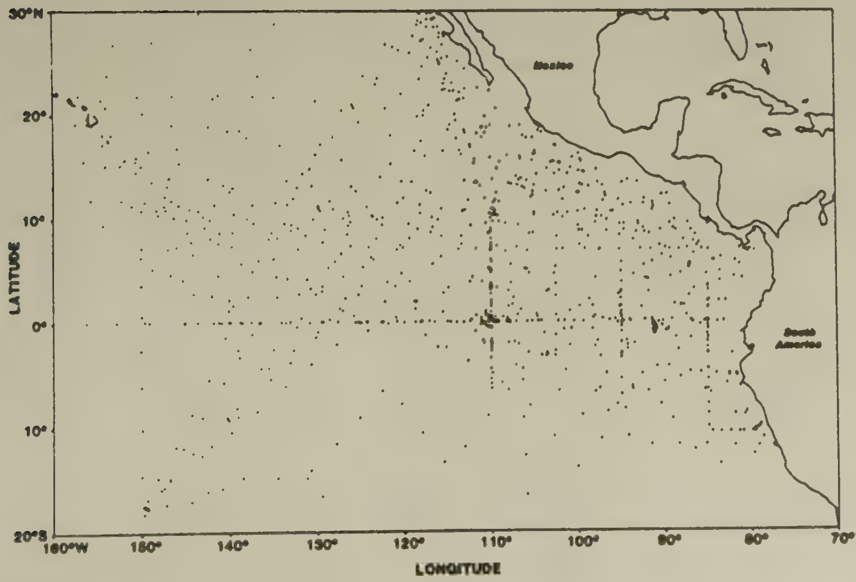

Figure 5.1. Noon positions of sea days during which a seabird watch was maintained.

Table 5.1. Percentage of seabird flocks associated with whale or delphinid cetaceans by area.

| | EASTERN SECTOR (COAST-125°W) | | | | WESTERN SECTOR (> 125°W–155°W) | | | |
|---|---|---|---|---|---|---|---|---|
| | | | *Pct. flocks with* | | | | *Pct. flocks with* | |
| *Center of 5° Latitude Intervals* | *Days observed* | *No. flocks* | *whales* | *delphinids* | *Days observed* | *No. flocks* | *whales* | *delphinids* |
| 25°N | 16 | 6 | 0 | 0 | | | | |
| 20°N | 14 | 11 | 0 | 73 | 21 | 7 | 0 | 0 |
| 15°N | 35 | 104 | 0 | 68 | 15 | 19 | 0 | 0 |
| 10°N | 54 | 133 | 2 | 35 | 27 | 23 | 0 | 30 |
| 5°N | 49 | 126 | 2 | 27 | 22 | 51 | 0 | 8 |
| 0° | 38 | 108 | 2 | 4 | 11 | 13 | 0 | 0 |
| 5°S | 14 | 80 | 0 | 5 | 7 | 6 | 0 | 0 |
| 10°S | 11 | 69 | 1 | 7 | 8 | 5 | 0 | 0 |
| 15°S | — | — | 0 | 0 | 5 | 1 | 0 | 0 |
| Total | 231 | 637 | 1 | 27 | 116 | 125 | 0 | 9 |

Notes: Flocks are defined as ≥ 10 birds; data from January–February cruises, 1977, 1979, 1980; percentages have been rounded; each latitude interval is defined by its center latitude ± 2.5°.

Table 5.2. Species composition and species diversity of flocks by area.

| Sector | Center of 5° Latitude Intervals | Total Birds | PERCENT SPECIES COMPOSITION |  |  |  |  |  |  |  |  | SPECIES DIVERSITY |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | boobies | sooty tern | WTSW | jaeger | frigate birds | LPT | other terns | other shear-waters | other petrels | $\frac{1^{a}}{\Sigma Pi^{2}}$ | Spp. per[b] Flock |
| Eastern (From Coast to 125°W) | 25°N | 151 |  |  |  | 1 | 10 |  |  | 68 | 21 | 1.96 | — |
|  | 20°N | 1,279 | 15 | 3 | 8 | 1 | + | 2 | 22 | 46 | 3 | 3.46 | 4.4 |
|  | 15°N | 13,035 | 50 | 4 | 30 | 11 | 2 | + | 1 | 1 | + | 2.80 | 4.0 |
|  | 10°N | 6,852 | 14 | 28 | 32 | 13 | 8 | 1 | 1 | 2 | + | 4.40 | 4.2 |
|  | 5°N | 9,358 | 42 | 20 | 13 | 2 | 5 | + | 17 | + | + | 3.75 | 3.3 |
|  | 0° | 4,092 | 7 | 90 | 1 | + | + | + | 1 | + |  | 1.22 | 1.2 |
|  | 5°S | 3,696 | + | 94 |  | + | 2 |  | 4 |  | + | 1.12 | 1.3 |
|  | 10°S | 5,366 | 6 | 47 |  | 1 | 1 | 2 | 43 |  | + | 2.43 | — |
|  | 15°S |  |  |  |  |  |  |  |  |  |  |  |  |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Western (From > 125°W to 155°W) | 25°N | | | | | | | | | | | | |
| | 20°N | 100 | 2 | 76 | | | 9 | 13 | | | | 1.66 | |
| | 15°N | 1,076 | + | 64 | 16 | 6 | | 10 | 1 | 3 | 1 | 2.23 | — |
| | 10°N | 3,355 | + | 69 | 8 | 2 | | 19 | + | 1 | + | 1.92 | 3.0 |
| | 5°N | 2,439 | + | 68 | 7 | 1 | | 15 | + | 1 | 7 | 2.02 | 2.7 |
| | 0° | 4,239 | | 88 | 4 | + | | 4 | 1 | 1 | 2 | 1.29 | 2.3 |
| | 5°S | 6,983 | 1 | 97 | 1 | + | 1 | | | | 1 | 1.07 | 2.2 |
| | 10°S | 2,576 | + | 52 | 1 | | 2 | + | 40 | + | 4 | 2.29 | — |
| | 15°S | 1,538 | + | 40 | | | 1 | | 57 | + | 2 | 2.07 | — |

NOTES: Flocks are defined as ≥ 10 birds; flocks were evaluated whether or not cetaceans were present; data from January–February cruises, 1977, 1979, 1980; percentages have been rounded: each latitude interval is defined by its center latitude ± 2.5°.

Abbreviations: WTSW = wedge-tailed shearwater; LPT = large pterodroma: Juan Fernandez/white-necked/dark-rumped petrels; + = small percent < 1.0.

[a] Simpson's Index.

[b] Mean spp. per flock weighted by flock size; dash indicates unreliable data; for dolphin-associated flocks, mean spp./flock was 4.4 (s = 2.0) in eastern sector and 1.9 (s = 1.2) in western sector (Au and Pitman 1986).

## *Dichotomy in the Pelagic Community*

Two distinct faunal communities involving seabird flocks occur in the ETP, and suggest a strong, regional change either in prey or in the responses of predators to prey. The dichotomy separates multispecies flocks often associated with delphinid cetaceans from virtually single-species flocks seldom with delphinids (i.e., dolphins and other small, toothed "whales"). This separation occurs between latitudes 0° and 5°N and approximately corresponds with the oceanographic division between the permanently warm (> 25°C) and low salinity (< 34°/p.p.t.) Tropical (Surface) Water and the Equatorial (> 34°/p.p.t.) and Southern Subtropical (> 35°/p.p.t.) waters (see Wyrtki 1966; Ashmole 1971).

### *Northern (Tropical Water) Flocks*

The Northern, or Tropical Water, flocks in the eastern sector were notable for frequently being with delphinid cetaceans: 68 percent and 73 percent of flocks from the 15°N and 20°N (± 2.5°) latitude intervals, respectively, were with delphinids (table 5.1). Associations with whales in these latitudes were infrequent (0–2 percent). These flocks (table 5.2) were typically multispecies aggregates of boobies—primarily red-footed *(Sula sula)*, masked *(S. dactylatra)*, and brown *(S. leucogaster)*—and wedge-tailed shearwaters *(Puffinus pacificus)*, sooty terns *(Sterna fuscata)*, and jaegers *(Stercorarius* spp.) (see appendix 5.1 for a list of species names). Boobies were most abundant, composing 42 percent and 50 percent of individuals in flocks in the latitude intervals centered at 5°N and 15°N. Their reduced importance about the 10°N interval was due in part to sampling near the Costa Rica Dome, a localized upwelling regime (Wyrtki 1964) that does not normally produce good catches of yellowfin tuna (the significance of which will be explained below).

In the western sector the northern flocks were associated with delphinids mainly within the 10°N interval (a much narrower zonation than seen to the east) where the association rate was 30 percent. As in the east, whales appeared unimportant to seabirds; none were seen with flocks. The species composition of these flocks was different from that of flocks farther to the east, and thus comprised a second type of multispecies community consisting mainly of sooty terns and Juan Fernandez/white-necked petrels (*Pterodroma externa externa/cervicalis*—subspecies that are difficult to separate in the field).

### *Southern (Equatorial and Southern Subtropical Water) Flocks*

South of the 5°N latitude interval, in Equatorial and Southern Subtropical waters, but primarily the latter, flocks in the eastern sector occurred infrequently with delphinid cetaceans (table 5.1), in sharp contrast to the northern multispecies flocks. The southern flocks were clearly dominated by sooty terns (table 5.2) which composed 90 percent or more of birds in flocks in the 0° and 5°S latitude intervals, mainly in the areas away from islands.

In the west none of the southern flocks encountered were associated with either delphinids or whales. The sooty tern was still the most abundant species, up to 97 percent of the birds in all flocks. White terns *(Gygis alba)* and noddy terns (*Anous* spp.) were an increasing component of the flocks in the far southern latitudes; the latter terns were especially abundant near islands.

## *Species Diversity Differences*

The transition and difference between the northern and southern seabird communities are reflected in latitudinal changes in species diversity. Values of Simpson's Dominance Index $\frac{1/\Sigma p_i^2}{p_i^2}$ where $p_i$ is the fraction of total birds that are species i) and of the average number of species per flock are given in the last two columns of table 5.2. Here the index could vary between 1.0 for flocks completely dominated by one species to 9.0 for flocks with individuals evenly divided among all nine categories of species. Simpson's Index is one of the more useful and easily understood measures for describing species in communities (Hill 1973) and shows that flocks in the northern latitude intervals, 20°N to 5°N, were on average 3.1 to 1.7 times more diverse than were flocks in the intervals 0° and 5°S, in the eastern and western sectors respectively. The southern flocks had index values close to 1.0 due to dominance by sooty terns. Data in the species per flock column suggest a decline in the average number of species from northern to southern latitudes (from ca. 4 to 1 spp./flock), at least in the eastern sector. Although there were difficulties in observing and identifying species from non–dolphin-associated flocks, this measure indicates areawide changes in diversity similar to those shown by Simpson's Index.

## Seabirds and Cetaceans

As a group, seabirds associate only with specific cetaceans, a fact reflecting an underlying, probably feeding, relationship. This is shown in table 5.3, a summary of schooling and bird association characteristics of ETP whales and delphinids, again mainly from the more representative 1977, 1979, and 1980 dolphin surveys. Study of this table will give the reader an appreciation of the structure of the pelagic community under discussion, including the relative abundance of the different Cetacea and the likelihood (percent occurrence) of finding particular bird species in the associated flocks. In judging relative abundance, however, one should remember that different species vary in their detectability according to their size (school and individual) and behavior (including association with birds).

### *Associations with Dolphins*

Of all Cetacea, spotted *(Stenella attenuata)* and spinner *(S. longirostris)* dolphins are associated most often with birds: 74 percent and 78 percent, respectively, of these species' schools were with flocks (table 5.3: first two species, col. 6). A high percentage of these schools included other cetaceans, 79 percent in the case of the spinner dolphin (col. 5). Most of this mixing involved these two species themselves: of the 113 spinner dolphin schools, 67 percent were mixed with spotted dolphins and of 206 spotted dolphin schools, 37 percent were mixed with spinner dolphins. Both of these dolphins occurred in large schools, averaging 150 and 133 individuals respectively (col. 3), and were associated with large flocks averaging 121 and 147 birds respectively (col. 7). The standard deviations (s) of these measures were large relative to the means, due to size distributions skewed toward the larger sizes. The bird species most likely present (high percent occurrence) in flocks with these dolphins were boobies (*Sula* spp.), frigate birds (*Fregata* spp.), wedge-tailed shearwaters, and jaegers, generally in that order. Spotted and spinner dolphins are diurnally active—i.e., fast swimming ("porpoising"), leaping often—and are frequently associated with yellowfin tuna. Both are pursued by purse seiners in "porpoise-tuna" fishing, a technique in which tuna are first caught with dolphins, then retained as the mammals are subsequently released.

Table 5.3. Summary of cetacean species encountered and their associations with seabirds: Characteristics of schools and flocks.

| | SCHOOLS | | | | | ASSOCIATED FLOCKS | | | |
|---|---|---|---|---|---|---|---|---|---|
| SPECIES | *n* | *x̄* | *s* | *Pct. mixed*[a] | *Pct. with flocks* | *x̄* | *s* | *Spp. of > 50% occur*[b] | COMMENTS |
| Spotted dolphin<br>*(Stenella attenuata)* | 206 | 150 | 177 | 40 | 74 | 121 | 219 | booby –82%<br>frigate –70<br>WTSW–57<br>jaeger –53 | Main target of "porpoise-tuna" fishing; diurnally active (leaping, fast swimming) sp.; mixed schools usually with spinner dolphin. Frequently with flocks; epipelagic prey (Perrin et al. 1973). |
| Spinner dolphin<br>*(Stenella longirostris)* | 113 | 133 | 207 | 79 | 78 | 147 | 258 | booby –73%<br>frigate –69<br>jaeger –62<br>WTSW–54 | Second most important dolphin in "porpoise-tuna" fishing; diurnally active, usually mixed with spotted dolphins; frequently with flocks. Epi- and mesopelagic prey (Perrin et al. 1973). |
| Common dolphin<br>*(Delphinus delphis)* | 62 | 129 | 176 | 6 | 39 | 38 | 46 | booby –70% | Less involvement in "porpoise-tuna" fishing; often escapes with tuna from nets; very active diurnally; third most frequent dolphin with flocks. May feed on deep prey (Fitch and Brownell 1968). |

Table 5.3. (continued)

| SPECIES | SCHOOLS | | | | | ASSOCIATED FLOCKS | | | COMMENTS |
|---|---|---|---|---|---|---|---|---|---|
| | *n* | $\bar{x}$ | *s* | *Pct. mixed*[a] | *Pct. with flocks* | $\bar{x}$ | *s* | *Spp. of > 50% occur*[b] | |
| Striped dolphin (*Stenella coeruleoalba*) | 139 | 54 | 62 | 9 | 7 | 15 | 24 | | Common, diurnally very active species in relatively small schools; seldom with birds or tuna. May feed on mesopelagic prey (Miyazaki et al. 1973). |
| Bottlenose dolphin (*Tursiops truncatus*) | 119 | 25 | 59 | 41 | 13 | 11 | 12 | | Often with *Globicephala, Grampus, Steno*; sometimes with *Stenella*; often approaches ships; not with large flocks. |
| Risso's dolphin (*Grampus griseus*) | 106 | 11 | 18 | 20 | 3 | 16 | 17 | | Often with *Tursiops, Globicephala*, traveling slowly. Seldom with birds. |
| Pilot whale (*Globicephala macrorhynchus*) | 98 | 14 | 12 | 37 | 4 | 11 | 11 | | Often with *Tursiops, Grampus*; appears to be resting much of the time. Seldom with birds. |
| Rough-toothed dolphin (*Steno bredanensis*) | 54 | 12 | 10 | 15 | 35 | 12 | 15 | booby –72%<br>frigate –72 | Sluggish behavior; often near flotsam; sometimes with *Tursiops, Globicephala, Grampus*; fourth most frequent dolphin with birds. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Melon-headed whale<br>*(Peponocephala electra)* | 4<br>(42 | 194 | 151 | 75<br>17 | 25<br>7)[c] | 1 | — | Diurnally active; often in large, dense schools with *Lagenodelphis*. Seldom with birds. |
| Fraser's dolphin<br>*(Lagenodelphis hosei)* | 10<br>(23 | 391 | 576 | 40<br>44 | 20<br>13)[c] | 2 | — | Often in large, densely packed, fast-moving schools with *Peponocephala*. Schools often execute coordinated turning and diving. |
| Pygmy killer whale<br>*(Feresa attenuata)* | 9 | 37 | 18 | 0 | 0 | — | — | Appears to rest during the day; may approach ships. Seldom with birds. |
| False killer whale<br>*(Pseudorca crassidens)* | 19 | 13 | 13 | 26 | 10 | 12 | 5 | Sometimes with *Tursiops*; will approach ships at high speeds; not with large flocks. |
| Killer whale<br>*(Orcinus orca)* | 8 | 7 | 4 | 12 | 12 | 20 | — | Small schools, usually loosely aggregated; not with large flocks. |
| Rorquals<br>(baleen whales)[d] | 94 | 2 | 1 | 3 | 3 | 43 | 27 | Generally feed near surface on small fish and crustaceans; seldom with birds. |
| Ziphiids<br>(beaked whales) | 85 | 2 | 2 | 1 | 0 | — | — | Deep feeder; shy and inconspicuous. Not with birds. |
| Sperm whale<br>*(Physeter macrocephalus)* | 63 | 8 | 7 | 8 | 2 | 2 | — | Deep feeders; sometimes in large aggregations. Rarely with birds. |
| Dwarf/pygmy sperm whale *(Kogia spp.)* | 30 | 2 | 1 | 0 | 0 | — | — | Difficult to see except in calm seas. Not with birds. |

NOTES: Numbers in table rounded for greater clarity; standard deviations not calculated for $n < 10$; birds counted regardless of flock size; n = number of schools, $\bar{x}$ and s refer to school or flock size.

Abbreviations, *see* table 5.2.

[a] i.e., school mixed with other cetacean sp.

[b] Listed here are bird spp. and their percentage occurrence in flocks associated with the given cetacean sp., provided the percentage was ≥ 50 and flocks ≥ 10 birds. WTSW = wedge-tailed shearwater.

[c] From larger sample from all research ship observations, and also including *Feresa* schools.

[d] Mostly Bryde's whale.

The common dolphin *(Delphinus delphis)* was the third most frequent species of dolphin found with bird flocks, although the percentage of its schools found with flocks was much lower (39 percent). This species also forms large ($\bar{x} = 129$), actively porpoising schools. Boobies, and also wedge-tailed shearwaters and frigate birds, often occurred in flocks associated with this dolphin. Fishermen do not regularly catch tuna with the common dolphin.

The last of the more frequently encountered, active delphinids, the striped dolphin *(Stenella coeruleoalba)*, is seldom found with birds. It usually occurred in fast-moving and often high-leaping, relatively small, unmixed schools ($\bar{x} = 54$) that were without indications of associated tuna. It is seldom deliberately fished on by purse seiners.

With two exceptions (see below) the remaining delphinids occur in small schools that are seldom with birds, and perhaps never with large flocks. Except for the false killer whale *(Pseudorca crassidens)*, all are relatively slow moving. And although the sluggish-behaving rough-toothed dolphin *(Steno bredanensis)* would seem to be an exception in that 35 percent of its schools were recorded with birds, we saw no evidence to indicate that this or any other other of these remaining dolphins occurred with tuna.

The melon-headed whale *(Peponocephala electra)*—sometimes called the electra dolphin—and Fraser's dolphin *(Lagenodelphis hosei)* are also seldom with birds, but yet they are like the bird-associated spotted and spinner dolphins in being diurnally active, fast moving, and in large schools ($\bar{x} = 194$ and 391, respectively), often mixed together. A sample from all research ship sightings between 1976 and 1981 that included all schools that were at least very likely either *Peponocephala* or *Feresa attenuata* (pygmy killer whale)—two species difficult to distinguish—gave twenty-three *Lagenodelphis* schools, of which only 13 percent were with bird flocks, and forty-two either *Peponocephala* or *Feresa* schools, of which only 7 percent were with birds (see bracketed results in table 5.3). It is clear, therefore, that birds are not strongly associated with any of these three dolphins.

### *Associations with Whales*

We sighted many species of whales, and found they are generally not associated with birds (table 5.3). The rorquals we observed included blue *(Balaenoptera musculus)*, minke *(B. acutorostrata)*, sei *(B. borealis)*, and Bryde's *(B. edeni)* whales; these occurred singly or in small groups, all rarely with flocks. The ziphiid, or beaked whales, were also in small groups and were never seen with birds. Sperm whales *(Physeter macrocephalus)*, occasionally in large groups, were only rarely with birds. The related pygmy/dwarf sperm whales (*Kogia* spp.) were not seen with birds.

## Seabirds, Dolphins, and Yellowfin Tuna

### *The Predominance of Spotted/Spinner Dolphins with Seabirds*

Clearly, only spotted and spinner dolphins in the ETP are commonly associated with seabirds, an indication of underlying behavioral interactions that are very species specific. This predominance is made clear in figure 5.2, which shows the percentage of schools of the different dolphins that were with flocks, as well as the percentage of all associated flocks occurring with each dolphin species. Separate histograms are given for latitudes 5°N to 30°N (Tropical Water) and < 5°N to 12°S (Equatorial and Southern Subtropical waters). Among the spotted and spinner dolphins, in mixed or in pure schools, schools with spotted dolphins were usually most often with birds, particularly in the 5°N to 30°N Tropical Water.

The relationship of birds to spotted dolphins appears to be stronger than that of birds to spinner dolphins. Of the 242 flocks in table 5.3, 63.2 percent were associated with at least some spotted dolphin as opposed to 43.0 percent with at least some spinner dolphin. Also, 34.7 percent of these flocks were with unmixed spotted dolphin but only 10.3 percent with unmixed spinner dolphin schools. Most spinner dolphin schools associated with birds (78 percent of 113 = 88 schools; table 5.3) were also with spotted dolphins (76.1 percent of 88). Flocks were less likely to be with unmixed spinner dolphin schools in northern tropical waters and more likely in waters to the south (figure 5.2). This was because most bird-associated spinner schools in the northern waters were also with the spotted dolphin.

While this strong relationship of seabird flocks to spotted and spinner dolphins is characteristic of the Tropical Water habitat north of the equator, and also of the area south of the Galapagos Islands during the southern summer (December to February), these dolphins are relatively infrequently with birds elsewhere (compare the two latitude intervals in figure 5.2). This is so particularly in areas southwest of the Galapagos Islands, in spite of the abundance of flocks there. Table 5.4 shows the reduction in equatorial and southern latitudes of both the schools of these two dolphins and the percent of these schools that were associated with flocks of more than ten birds.

## *The Yellowfin Tuna Link*

### *Tuna Under Flocks*

Seabirds in flocks appear to feed mainly on prey driven to the surface by tunas, which are the only sizable pelagic fishes known to form abundant and large surface schools in the tropical ocean. Not infrequently we have been able to identify the predatory fish under

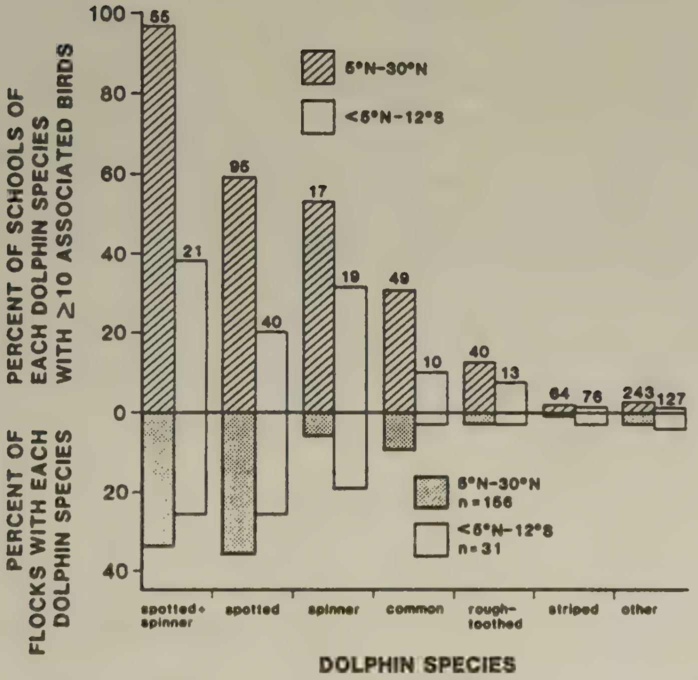

Figure 5.2. The rate of association of different dolphins with bird flocks (above) and the percent of these dolphin-associated flocks with each dolphin species (below) Numbers over the bars are the schools examined.

Table 5.4. Areawide differences in the percentage of spotted and spinner dolphin schools with bird flocks.

| Center of Latitude Intervals | COAST TO 125°W |  |  | > 125°W TO 155°W |  |  | TOTALS |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  | *Schools with flocks* |  |  | *Schools with flocks* |  |  | *Schools with flocks* |  |
|  | *Schools* | *n* | % | *Schools* | *n* | % | *Schools* | *n* | % |
| 20°N | 9 | 3 | 33 |  |  |  | 9 | 3 | 33 |
| 15°N | 76 | 51 | 67 |  |  |  | 76 | 51 | 67 |
| 10°N | 50 | 33 | 66 | 11 | 5 | 46 | 61 | 38 | 62 |
| 5°N | 67 | 32 | 48 | 3 | 3 | 100 | 70 | 35 | 50 |
| 0° | 28 | 3 | 11 | 3 | 1 | 33 | 31 | 4 | 13 |
| 5°S | 15 | 3 | 20 | 1 | 0 | 0 | 16 | 3 | 19 |
| 10°S | 6 | 5[a] | 83 | 3 | 0 | 0 | 9 | 5 | 56 |
| Total | 251 | 130 |  | 21 | 9 |  | 272 | 139[b] |  |

NOTES: Data from research cruises in 1976, 1977, 1979, 1980; some schools near land are deleted; flocks are of size ≥ 10 birds. Each latitude interval is defined by its center latitude ± 2.5°.

[a] These associated flocks were encountered south of the Galapagos Islands and west of Peru, where the porpoise-tuna fishery extends during the southern summer.

[b] 58.8% of schools in latitude intervals ≥ 5°N (± 2.5°) were with flocks of size ≥ 10; only 21.4% of schools in latitude intervals < 5°N (± 2.5°) were with such flocks. This differential is significant ($X^2$, $P < 0.005$).

a feeding flock as tuna (see also Murphy and Ikehara 1955; Ashmole and Ashmole 1967). The strongest evidence linking birds and dolphins to tuna is the existence of the "porpoise-tuna" fishery of the eastern Pacific, in which purse seiners catch yellowfin and to a lesser extent skipjack *(Katsuwonus pelamis)* tuna that swim with dolphins. These tuna, and the associated dolphins, are found mainly by searching the horizon for birds. Spotted, spinner, and common dolphins (ranked by importance) are the primary cetaceans involved in that fishery (Hammond 1981; Smith 1979). These are the same species, and order of importance, of dolphins that are associated with bird flocks, indicating that birds and dolphins are associated because of a tuna relationship.

*The "Porpoise-Tuna" Fishery*

The extent of the fishing grounds for surface-caught yellowfin is shown in figure 5.3 with the distribution of sightings of spotted dolphin superimposed (the distribution of spinner dolphin is nearly the same). The similarity of these distributions indicates an intimate species interaction, although such a result could be an artifact of joint fishing on both species by the purse seiners that supplied the data to the SWFC. However, the general pattern of the dolphin distribution has been confirmed by fishery-independent surveys (Au and Perryman 1985). Dolphin-associated yellowfin tend to be large ($\bar{x} = 120$ cm, $s = 22$ cm, years 1981–85) (see also Allen 1985) with sizes overlapping into the range of smaller yellowfin not caught with dolphins and of larger, deep-dwelling yellowfin that are caught by longline gear. Appendix 5.2 shows the relationship between tons of yellowfin caught and sizes of the associated dolphin schools on the purse seine grounds. The porpoise-tuna fishery indicates that seabirds and dolphins are linked via a relationship (probably feeding) with large yellowfin tuna.

## The Ecology of Flocks

### *Species in Dolphin-Associated Flocks*

*Composition*

The species composition of dolphin-associated flocks shows the same regionwide differences among flocks in general. The important bird species that make up flocks associated with spotted and spinner dolphins are shown in figure 5.4, where again the histogram is separated for latitudes 5°N to 30°N and 5°N to 12°S. As in table 5.2, boobies, wedge-tailed shearwaters, jaegers, sooty terns, and frigate birds were numerically most important, in that order, in the dolphin-associated flocks from the northern Tropical Water habitat (5°N–30°N).

In the southern waters (< 5°N–12°S) boobies and sooty terns predominated; however, they were not usually in the same flocks. Boobies occurred mainly in flocks not too distant from coasts, while the sooty tern—more usually in virtually single-species flocks not with dolphins—was characteristic of the far offshore flocks (tables 5.1, 5.2).

*Species Associations*

Boobies, wedge-tailed shearwaters, jaegers, and frigate birds were found to be positively associated in dolphin-associated flocks from the Tropical Water purse seine fishing grounds, while frigate birds and sooty terns were positively associated in mainly the outer areas

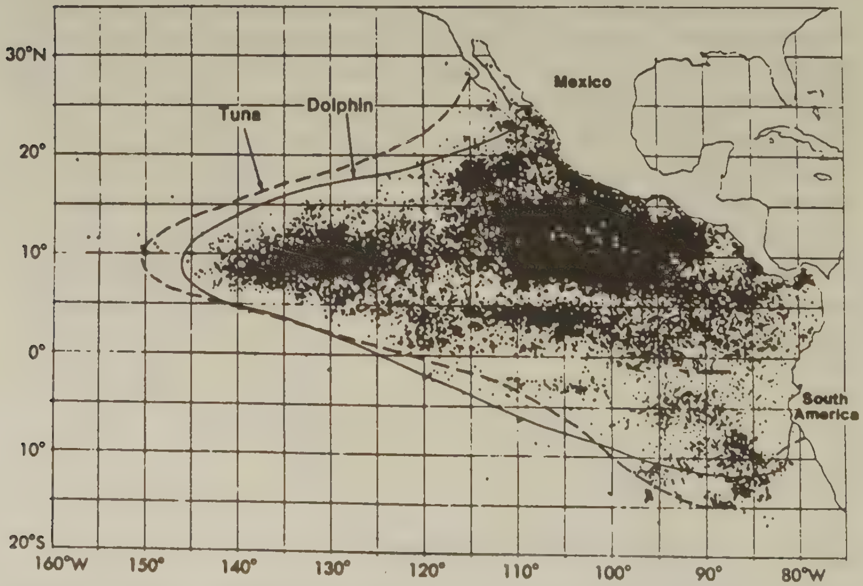

Figure 5.3. The distribution of records of spotted dolphins (dots and solid boundary, after Perrin et al. 1983) in relationship to the yellowfin tuna purse seiner grounds (dashed boundary, after Calkin's (1975) map of areas that produced 25+ tons of yellowfin catch).

of that habitat (Au and Pitman 1986). Table 5.5 is an extract of that analysis, showing percent co-occurrence of different bird species both in those flocks in which the species occurred, and in all flocks. The significant positive associations are also indicated. A schematic interpretation of this association complex is given in figure 5.5, where two measures of strength of association between species pairs are presented: Cole's (1949) coefficient and Yule's contingency index (see Pielou 1969:164). Our data indicate that none of the associations are very strong. The figure suggests that frigate birds are positively associated with other species in all habitats. The simplest explanation of these positive associations is attraction to common feeding opportunities.

## *Feeding Tactics/Strategies*

### *Multispecies Flocks and Facultative Commensals*

Within multispecies flocks, simultaneously different, species-specific feeding behaviors suggest prey aggregations that are diverse

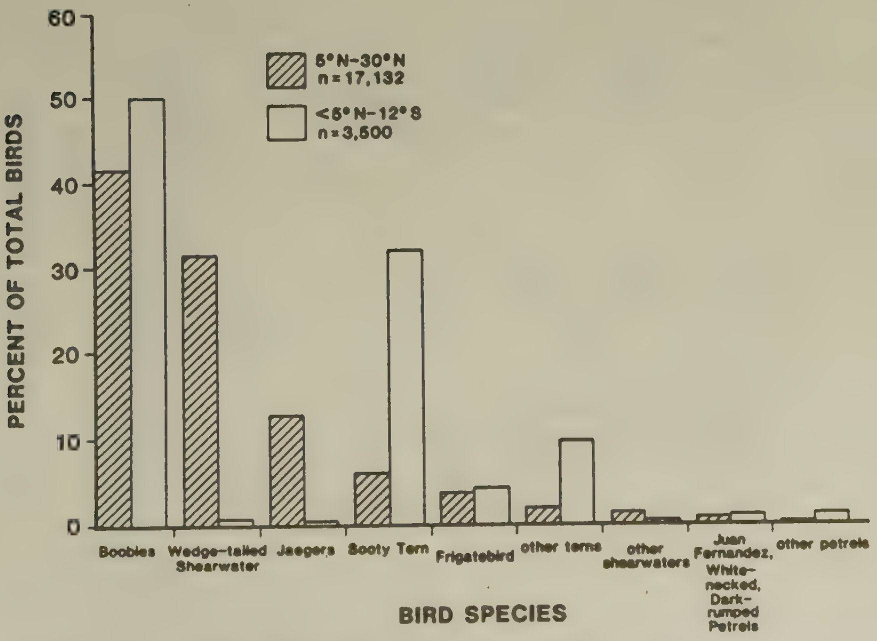

Figure 5.4. Likelihood (percentage frequency) of finding bird species in flocks associated with spotted and spinner dolphins.

Table 5.5. Percentage of co-occurrence of species pairs in flocks.

| | | *Boobies*<br>*n = 111* | *Frigate Birds*<br>*n = 90* | *WTSW*<br>*n = 82* | *Large Pterodromas*<br>*n = 18* | *Jaegers*<br>*n = 80* |
|---|---|---|---|---|---|---|
| Sooty tern | % n | 45 | 53* | 49 | 56 | 46 |
| | (% total) | (38) | (37)* | (31) | ( 8) | (28) |
| Boobies | % n | | 90* | 90* | 44 | 92* |
| | (% total) | | (62)* | (56)* | ( 6) | (56)* |
| Frigate birds | % n | | | 72 | 50 | 75 |
| | (% total) | | | (45) | ( 7) | (46) |
| WTSW | % n | | | | 50 | 74* |
| | (% total) | | | | ( 7) | (45)* |
| Large Pterodromas | % n | | | | | 11 |
| | (% total) | | | | | ( 7) |

NOTES: From $n = 131$ flocks associated with spotted or mixed spotted and spinner dolphin schools in latitudes 5°N–30°N in the eastern Pacific; example: sooty terns co-occurred with boobies in 45 percent of the 111 flocks containing boobies, and in 38 percent of all 131 flocks; * indicates a significant positive association between the species pair (by $X^2$, $P < 0.05$); there were no significant associations detectable among the thirty-three spotted/spinner dolphin–associated flocks from latitude < 5°N.

WTSW = wedge-tailed shearwater.

with respect to behavior, distribution in the water column, size, or species composition (we will refer to this diversity as prey "configuration"). Boobies, flying rapidly back and forth, especially over the advancing front of a tuna school, wheel and plunge after their prey or make midair captures. Wedge-tailed shearwaters seemingly race with the boobies, but at lesser heights, and then drop to the water in surface plunges or for contact dipping or surface seizing of prey that appear available for at least several seconds. Jaegers, taking prey by aerial pursuit and dipping, and occasionally by piracy, add to the scene of frantic activity (feeding methods are defined by Ashmole [1971]). By rapidly covering the school, birds of each species increase their encounter rate with unpredictably available and fleeting prey. Sooty terns employ another tactic—they watch widely and deep into the water for developing feeding opportunities from positions high above. Their prey appear to be grouped, for the entire

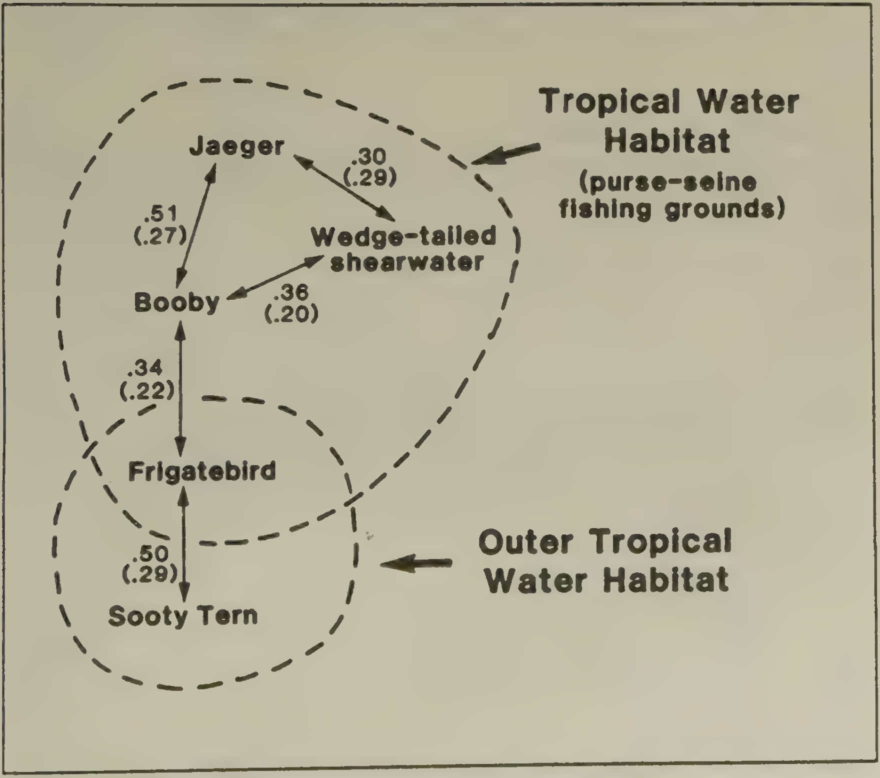
Tropical Water Habitat
(purse-seine fishing grounds)
Jaeger
.30
(.29)
.51
(.27)
Wedge-tailed shearwater
Booby
.36
(.20)
.34
(.22)
Frigatebird
.50
(.29)
Sooty Tern
Outer Tropical Water Habitat

Figure 5.5. Positive species-association links within flocks, with strength-of-association coefficients (Cole's and Yule's [in parentheses] coefficients) shown.

flock will swoop down synchronously. Frigate birds soar high above the feeding melee and swoop down at opportune moments after individual prey that are likely larger than that of the terns.

Except for sooty terns and frigate birds, most birds that occur in these multispecies flocks are facultative commensals with tuna. When feeding independently, these birds occur singly or in small groups, and aerial feeding is rarely seen. Petrels and shearwaters, for example, then rely more on scavenging or preying upon free-floating organisms such as *Velella* (Pitman personal observations). Boobies, however, appear to feed independently of tuna the least, and their distribution most closely coincides with that of the yellowfin tuna fishery (cf. figures 5.3 and 5.6, considering also the low-density, westward extension of booby habitat [below]). Boobies are both the most abundant of birds in flocks over tuna and dolphins (figure 5.4) and the most abundant of seabirds in the northern Tropical Water (Pitman 1986), with colonies in the eastern Pacific that are probably the world's largest (Nelson 1978). The abundance of boobies is likely a direct consquence of their strong association with yellowfin.

### *"Obligate" Commensals*

In contrast to the facultative commensals, sooty terns and frigate birds are almost never seen feeding independently of tuna in oceanic

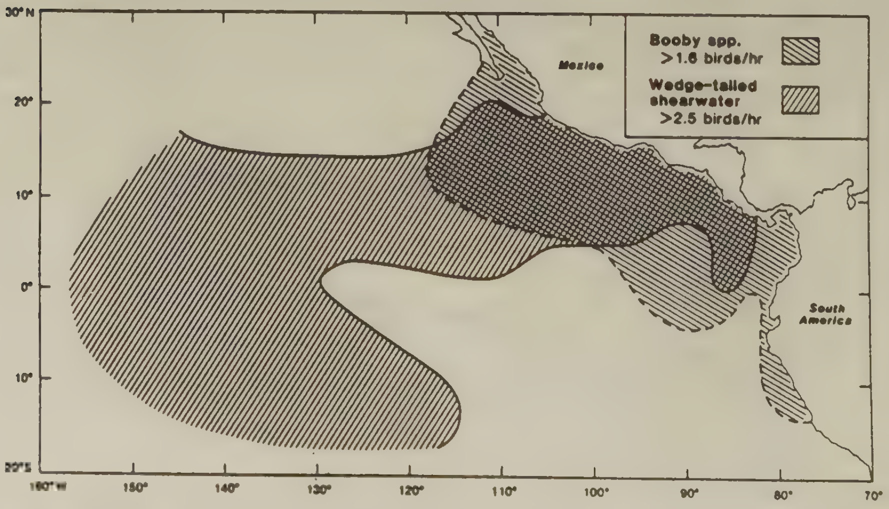

Figure 5.6. Booby and wedge-tailed shearwater habitats. Each shaded area delimits regions of greater than median sighting rate of the species (birds/hour). After Pitman 1986.

areas; they appear to be near-obligate commensals with these fish. The sooty tern, in particular, is most abundant beyond the yellowfin fishing grounds, where the tuna it feeds with are generally small, probably skipjack (Hida 1970), but possibly also frigate mackerel (*Auxis* spp.; see Olson and Boggs 1986) or small yellowfin and bigeye tuna *(Thunnus obesus)*. It is the most abundant seabird of the southeastern and central Pacific (Pitman 1986; Gould 1974). In the former area, there is apparently little opportunity for feeding independently of tunas; facultative commensals (i.e., most other birds) are virtually excluded from those waters, apparently being unable to feed either with sooty terns or independently (table 5.2 and below). The obvious ecological success of the sooty tern probably stems from its ability to follow and feed with the small tuna.

## *Feeding Regimes*

### *Species Distribution*

Distinctly different distributions of four birds that occur in flocks illustrate how the community dichotomy is formed from seabirds that seem to feed differently. The distributions are depicted in figures 5.6 and 5.7, where a single contour is used to enclose areas of higher population density of each species. These were derived from distribution and relative abundance studies by Pitman (1986). Each species' contour approximately delimits areas where densities were greater than that species' median sighting rate (birds per hour). Figure 5.6 shows boobies and wedge-tailed shearwaters inhabiting the Tropical Water north of the equator, but seldom occurring in a large area of the southeastern tropical Pacific west of the Peru Current. The habitat of the wedge-tailed shearwater extends into the eastern Pacific from broad areas to the west, while that of boobies extends from the east, westward with the yellowfin tuna fishing grounds. The lower-density (less than median sighting rate) habitat of boobies (primarily the masked booby) extends far west of Clipperton Island—at 10°N, 109°W (Pitman 1986) (this is not shown clearly in figure 5.6 because areas of greater than median sighting rate of boobies, especially the red-footed booby, are compressed toward the American coasts). Figure 5.7 shows an extensive high-density area of the sooty tern habitat in the central Pacific, extending into the Subtropical Water of the southeastern Pacific, the area with a dearth of boobies and wedge-tailed shearwaters. The high-density areas of this tern are sparse in the Tropical Water north of the equator. Finally, Juan Fernandez/white-necked petrels occur in a band about latitude 10°N, especially to the west of longitude 110°W.

Not shown is the jaeger habitat, mainly within a thousand-kilometer-wide band along the coast of Middle America, and the fact that the larger seabirds are relatively uncommon along the equator, being replaced there by plankton-feeding storm petrels. The distributions of the seabirds also vary seasonally; in particular, sooty terns probably extend farthest into the southeastern Pacific during the southern summer.

*Regional Prey Differences*

The northern (Tropical Water) and the southern (Equatorial and Southern Subtropical waters) habitats of the ETP thus appear to have different prey characteristics or configurations that require different foraging tactics, as indicated by community differences in seabird species and their interactions. In the northern Tropical Water, prey patches appear to be relatively large and to have diverse kinds of prey. Once found, hundreds of birds and dolphins (see table 5.3) and yellowfin (e.g., 10 tons of fish 60 lbs or greater; see IATTC 1984 and appendix 5.2) may feed upon the patch. Feeding many continue for some time (we have watched this activity for nearly an hour before continuing on). Under such conditions, satiated birds, e.g.,

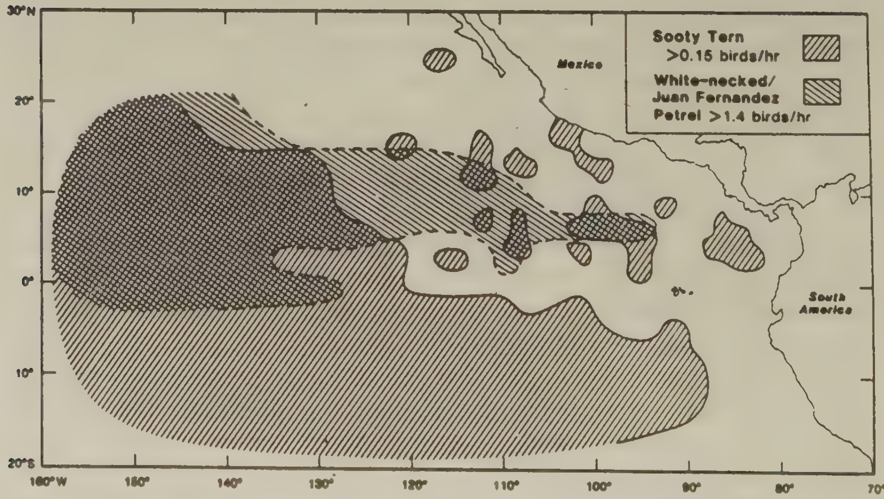

Figure 5.7. Sooty tern and white-necked/Juan Fernandez petrel habitats. Each shaded area delimits regions of greater than median sighting rate of the species (birds/hour). After Pitman 1986.

boobies, petrels, and especially shearwaters, may rest upon the water while others continue to feed (personal observation). In contrast, prey in the less productive southeastern and central Pacific appear to be in small, ephemeral, and thinly scattered patches of simple configuration, judging by the behavior and composition of feeding flocks. The buoyantly flying sooty tern especially, which is unable to rest long, or at all, upon the water, is evidently adapted for exploiting such prey, whose availability appears to change quickly, lending few opportunities for heavy feeding. These habitat differences probably reflect dissimilarities in biological productivity. The northern Tropical Water is richest because of its proximity to land and mechanisms that carry nutrients across its strong, shallow thermocline (Brandhorst 1958; Wyrtki 1966).

### *Pertubations*

If prey characteristics select for particular bird-tuna-dolphin interactions, environmental perturbations could alter these behaviors through effects on forage. During the 1982–83 El Niño warming event in the Pacific (Philander 1983), fishermen experienced a 25 percent reduction in the yellowfin tuna catch (IATTC 1984) and reported fewer porpoise-tuna schools. Because El Niño episodes usually result in reduced biological production and a deepened thermocline (see Barber and Chavez 1983), a weakened tuna-dolphin association might be expected, as is characteristic of the deep-thermocline and less productive southeastern and central Pacific. We looked for such effects in the characteristics of flocks recorded off Middle America (from Baja California to the equator) in 1979, 1980, and 1983. Records of all flocks and of flocks associated with spotted, spinner, and common dolphins were examined. These data, summarized in table 5.6, suggest that flock density was similar over the years, as was species composition: boobies and wedge-tailed shearwaters were always most abundant. However, flock size, dolphin school size, the percent of dolphin schools with birds, and the ratio of size of dolphin-associated flocks to that of all flocks were all much reduced in 1983. Although the 1983 sample was probably too small to be representative, these reduced percentages in 1983 are consistent with the idea that decreased food production or availability near the surface results in tuna feeding more independently of dolphins and in ways that are less useful to birds.

## General Discussion

It is curious that the association of seabirds, yellowfin tuna, and dolphins is so specific to spotted and spinner dolphins; the birds essentially ignore the twenty or so other species of Cetacea in the eastern Pacific. This is somehow related to the conspicuous partitioning of the eastern tropical Pacific (ETP) into distinct epipelagic communities of differently interacting predators.

### *Foraging Tactics and Species Interactions*

#### *Tuna Strategy and Consequences*

To begin understanding oceanic species interactions, it is useful to consider the behavior of the surface-schooling tunas. Tuna behavior exemplifies a strategy for exploiting the relatively sparse prey of tropical seas. Tropical tunas feed on epipelagic fish, squids, and crustaceans, whose distributions are undoubtedly very patchy with low overall densities (Blackburn 1968). To ensure a sufficient capture rate of such prey, tunas search by extensive ranging in the horizontal dimension, an energetically demanding tactic. Norberg (1977) postulated that as prey density decreases, the search method required of a predator increasingly becomes both more energy consuming and more efficient. Thus tunas have evolved into perhaps the most streamlined of fishes; their whole morphology and physiology appear designed for fast, sustained swimming with metabolic rates probably higher than those of all other fishes (see Sharp and Dizon 1978 for descriptions of energetics and hydrodynamics). High energy expenditure to obtain moderate energy returns from low-density prey must constrict the tunas' positive energy balance, narrowing the scope, or margin, between energy gained from food and energy consumed (see Warren and Davis 1966). Constriction of this energy margin increases vulnerability to natural mortality; for their size and speed, tropical tunas are remarkably short-lived, living probably less then ten years on the average (Beverton and Holt 1959).

These costs notwithstanding, the efficacy of the tunas' feeding strategy is evident; they are the dominant pelagic fishes of the tropical ocean, supporting extensive bird populations and productive fisheries. During the period 1974 to 1981 (between major El Niño events) an average of 196,000 metric tons of yellowfin tuna was harvested annually from the ETP, virtually all from surface or near-surface schools (IATTC 1984), approximately half of which were dolphin-associated (Allen 1985). In the same period, skipjack tuna produced an average annual catch of 122,000 metric tons, mainly from "schoolfish," i.e., surface schools without dolphins.

### *Feeding with Tuna*

Seabirds that feed with surface tunas exploit the tunas' tactic for finding prey and their habit of driving it to the surface. This role was recognized by Ashmole and Ashmole (1967) and is the basis for fishermen's reliance on birds to locate these fish. The degree to which tuna schools are accompanied by flocks, however, is difficult to estimate, as most schools are detected only if associated with birds. Appendix 5.3 shows that whereas most schools fished ~~by~~ seiners were with birds (as expected), schoolfish tuna were both less often and more variably with birds (29 percent to 77 percent overall depending upon area).

Dolphins that associate with yellowfin tuna also may have a feeding relationship with these fish. The prey of the spotted dolphin is similar to that of yellowfin, both feeding diurnally upon epipelagic fishes and squids (Perrin et al. 1973; Reintjes and King 1953). Seabirds feed on much the same kinds of prey (Harrison, Hida, and Seki 1983; Diamond 1983). Spinner dolphins feed more on mesopelagic animals and may be less directly linked to tuna (Perrin et al. 1973). The ecological success of spinner and especially spotted dolphins in the eastern Pacific, which may be appreciated by comparing the numbers and average sizes of their schools with that of the

**Table 5.6.** Comparison of flock characteristics and interactions off middle America during three years.

| | TOTAL | | | | |
|---|---|---|---|---|---|
| *Year* | *Flocks* | *Birds* | *Hours observed* | *Flocks per hour* | *% Flocks with dolphins* |
| 1979 | 136 | 10,366 | 270.0 | 0.5 | 27 |
| 1980 | 73 | 3,721 | 191.6 | 0.4 | 45 |
| 1983 | 25 | 800 | 49.0 | 0.5 | 28 |

NOTE: Dolphins referred to are spotted, spinner, and common dolphins.
WTSW = wedge-tailed shearwater.

other cetaceans (table 5.3), is likely due to a considerable advantage gained from feeding with yellowfin tuna.

*Seabirds' Relationship to Cetaceans*

In spite of the strong association of spotted and spinner dolphins with birds, our observations indicate that cetaceans themselves have little role in making prey available to seabirds. It is the tuna, primarily, that appear to drive prey to the surface, whether or not dolphins are present; foraging birds are almost always most active where the tuna are feeding, which often is at the leading edge of the school. This has been seen from ships (personal observation) and from helicopters (Au and Perryman 1982; Hewitt and Friedrichsen ms.). Thus spotted and spinner dolphins are commonly with birds because they swim with tuna with which the birds feed. And the common dolphin is relatively infrequently found with flocks because its association with tuna is similarly infrequent. Though the rough-toothed dolphin is not uncommonly associated with small flocks, it was probably the flotsam (and associated fish) near which this species was often encountered, rather than tuna or the mammals, that attracted the birds. Tropical seabirds thus appear to strongly associate only with those dolphins that swim and feed with tuna, dolphins that, like the tuna, are fast traveling and in large, diurnally active schools. Even so, these tuna and birds appear to feed independently of dolphins much of the time, as indicated by the delphinid association rate of flocks: between latitudes 2.5°N and 22.5°N, 58 percent of flocks (presumably with tuna) were not with dolphins (data for table 5.1, Eastern Sector). The tuna-dolphin association is

| PERCENT SPP. COMPOSITION OF FLOCKS | | | | | | | | FLOCK SIZE | | DOLPHIN SCHOOLS | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Boobies* | *Sooty tern* | *Other tern* | *WTSW* | *Other shear-waters* | *Jaegers* | *Frigate birds* | *Other birds* | *All* | *With dolphins* | *Size* | *Pct. With birds* |
| 38 | 13 | 3 | 34 | 1 | 8 | 2 | 1 | 76.2 | 159.8 | 297.9 | 75 |
| 23 | 17 | 12 | 15 | 1 | 11 | 7 | 3 | 51.0 | 88.4 | 149.2 | 76 |
| 16 | 1 | 10 | 66 | 2 | 4 | 2 | 0 | 32.0 | 21.7 | 115.2 | 29 |

clearly not obligatory; it seems rather to indicate an intersection or overlap of certain foraging tactics adopted by these species to exploit local prey configurations.

### *Communities and Foraging Requirements*

The foraging tactics required in a particular environment seem to shape communities by placing stringent demands upon the behavioral or energetic capabilities of predators, especially in biologically sparse waters. Thus while spotted and spinner dolphins regularly associate with large yellowfin tuna on the purse seine fishing grounds of the Tropical Water habitat, these tuna are largely unable to forage in the surface layer beyond those grounds, perhaps in part due to physiological needs (see Sharp 1978 for a detailed discussion), and the dolphins there seem unable to feed with the skipjack or other small tuna that replace the yellowfin. The multispecies flocks of both facultative and obligatory commensals that feed with yellowfin on the purse seine grounds are reduced to mainly sooty terns and wedge-tailed shearwaters in the biologically sparse waters of the central Pacific and to virtually sooty tern–only flocks, obigatorily commensal on small tuna, in the Southern Subtropical Water. Like other facultative commensals, wedge-tailed shearwaters, so widespread in the central Pacific (Pitman 1986; King 1974b), are apparently unable to assume the required feeding tactics and to penetrate the Southern Subtropical Water of the eastern Pacific (figure 5.6).

## *Who Follows Whom?*

It is clear that seabirds follow and benefit from feeding with tuna, but where these tuna are also associated with certain dolphins, does either the tuna or dolphin provide benefit to the other? This question is pertinent to understanding the role of dolphins in bird-tuna-dolphin associations. A widely held view is that tuna follow dolphins in foraging. Tuna evidently do follow dolphins that are chased by purse seiners and are eventually captured with these schools. Mullen (1984) showed how two potentially competing predators could theoretically and stably coexist in a commensal relationship and suggested that the tuna were commensals on the dolphins. But perhaps tuna, and pelagic schooling fishes in general, obtain protection from pursuing predators by crowding under objects they normally encounter, both animate and inanimate—as when a predacious marlin approaches, skipjack will hide under the boat fishing them (D. Correa, personal communication). We suggested (Au and Pitman 1986) that spotted and spinner dolphins follow yellowfin in jointly foraging schools, inferring this mainly because seabirds are often seen feeding at the front of such schools in immediate association with the tuna rather than the dolphins. We note that the tuna-dolphin association breaks down outside the ETP purse seine grounds, where large yellowfin no longer commonly school at the surface (the dolphins must continue to do so, though they are no longer often with birds), and that a large tuna school, searching in three-dimensional space and perhaps using olfactory cues, could be more efficient than dolphins in locating prey.

In retrospect, it seems unlikely that a simple answer, either the dolphins or the tuna following the other to food, could be satisfactory. Neither is it likely that the tuna-dolphin-bird association merely results from the convergence of predator species upon the same food patches, for the association is too species specific, and tunas and dolphins appear to travel together, even while not actively feeding. Finally, no explanation can be satisfactory unless it also explains why the dolphin-tuna association is not characteristic of the eastern tropical Atlantic (Levenetz, Fonteneau, and Regalado 1980; Stretta and Slepoukha 1986), where a large purse seine fishery for surface yellowfin and skipjack tuna also exists, and dolphins similar to that of the ETP occur (Leatherwood, Caldwell, and Winn 1976).

## *A Feeding Tactics Hypothesis*

### *Hypothesis*

We propose a hypothesis that particular prey configurations or arrangements that are a function of productivity shape species interactions through the foraging tactics required to exploit that prey. The resulting explanation of species interactions is as follows: In low productivity waters, low-density prey are exploited by skipjack or similar small-sized tuna that are specialists at surviving on small prey from highly dispersed, relatively small patches. These patches are sufficiently encountered only through the most rapid and energetically expensive, wide-ranging search. Under such conditions smaller, rather than larger, predators are at an advantage (Norberg 1977). In accordance with foraging theory (Charnov 1976), these tuna employ, in effect, hit-and-run tactics on patches not much more profitable than from average searching between patches. Ecologically successful seabirds in such areas would be those capable of keeping up with these fast tuna, there being little food available independent of the fish.

In areas of intermediate food productivity, such as along oceanic boundary zones, food patches and prey are larger, though still best discovered by extensive horizontal ranging. Once found, these patches often provide for relatively long feeding bouts. Large yellowfin tuna and similarly foraging spotted and spinner dolphins find and exploit this prey, often jointly. When doing so, the tuna may be the primary predator, and they may drive some prey to the surface. Many birds take advantage of these enhanced feeding opportunities, forming multispecies flocks; however, most species in these flocks can also supplement their food by also feeding independently of tuna.

In still higher-productivity waters, such as coastal areas, prey is more diverse, the food encounter rate is high, prey patches are large and more predictable, and the advantage of the wide-ranging foraging tactic of tunas is lessened. It may sometimes be advantageous for tunas to forage passively—for example by waiting for prey under objects. The richer and less clumped food resources would enable the different predators to specialize and to feed more independently.

### *Extensions*

The hypothesis would predict that reductions in food productivity would reduce the participation of all species involved in joint feeding, as suggested for 1983 in table 5.6 (this would not be expected if there were an obligate commensal relationship between tuna and dolphins). Moreover, the switching of feeding tactics and hence changes in community interactions might be the mode of response to such changes. Such a mechanism may have been involved in the massive population failure of seabirds from Christmas Island during the last El Niño (see Schreiber and Schreiber 1984).

The hypothesis suggests that intermediate productivity would be most conducive to the formation of multispecies interactions involving birds, tuna, and dolphins. In fact, the most extensive porpoise-tuna fishing areas in the eastern Pacific are not the rich coastal and upwelling-influenced waters off Central America, but the warm, stable waters off southern Mexico and the waters west of Clipperton Island. Areas where two-thirds or more of purse seine operations are on dolphin-associated yellowfin begin about 600 kilometers offshore (see Allen 1985), except off southern Mexico, where the fishing comes close to shore. Could it be that yellowfin tuna in the eastern tropical Atlantic are seldom associated with dolphins because waters there are not sufficiently intermediate in productivity to develop the right prey configuration? That fishery is located mainly in the Equatorial Counter and Guinea currents within 500 kilometers of the southern West African coast, an environment more similar to Pacific waters west of Panama and Colombia than to the ridged thermocline (Cromwell 1958), offshore porpoise-tuna grounds west and southwest of southern Mexico (see Merle 1978).

### *Background*

This idea, that the resource base in different environments controls species interactions through the tactics required for its exploitation, is patterned after the concepts developed by Crook (1965) in a study on birds and as applied in comparative behavior studies of primates (Crook 1970; Clutton-Brock and Harvey 1977). These authors explained how the social organization and behavior of species are shaped by the availability of food and sites for reproduction. Smith et al. (1986), noting that common dolphins tended to occur in large, mobile schools in oceanic waters off California, while Dall's porpoise *(Phocoenoides dalli)* occurred in small, relatively sedentary schools in chlorophyll-rich, coastal waters, suggested that the behavioral and population differences were due to feeding strategies required of each species in the different environments. Differences in feeding behaviors of seabirds from Antarctic to tropical seas were explained by Ainley and Boekelheide (1983) as adaptations to regional differences in prey density and patchiness, as well as to the presence of subsurface competitors and predators. Wiens (1984) reviewed the importance of resources in the organization of avian populations and communities, noting how little direct evidence there was of resource limitation. He cautioned against imposing possibly preconceived processes, such as competition, on the analysis of relationships. However, Safina and Burger (1985) thought that terns in coastal waters could compete with bluefish by pursuing the same individual prey. We have not directly considered competition as a mechanism in our hypothesis. Until demonstrated, Schoener's hypothesis (1982) of predator convergence onto locally abundant prey patches, with little interspecies competition, seems more likely. Ours is an attempt to explain the existence in the eastern tropical Pacific of distinct pelagic communities, not separated by physical barriers, and composed of specific assemblages of highly mobile species with specific behavioral interactions.

## Summary

Two distinct faunal communities involving seabirds may be recognized in the eastern tropical Pacific. One, characteristic of the Tropical Water habitat mainly north of latitude 5°N, consists of multispecies flocks of primarily boobies, wedge-tailed shearwaters, jaegers, and sooty terns. These flocks are frequently associated with large yellowfin tuna and dolphins. Of the dolphins, the spotted and spinner species predominate (ca. 75 percent of dolphin-associated flocks involve these two species). These dolphins appeared to be linked to birds because both feed with large yellowfin tuna wherever the latter forage close to the surface. The other community occurs primarily in Subtropical Water to the south and consists of virtually single-species flocks of sooty terns. These flocks are associated with small tuna but seldom with dolphins. We propose that the different kinds of species associations seen in the eastern Pacific are manifestations of different foraging tactics required of pelagic predators in the different areas, and that the intersection of such tactics could explain the bird-tuna-dolphin association.

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### References

Ainley, D. G. and R. J. Boekelheide. 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. In R. W. Schreiber, ed., *Tropical Seabird Biology*, pp. 2–23. Cooper Ornithological Society, Studies in Avian Biology, no. 8.

Allen, R. L. 1985. Dolphins and the purse-seine fishery for yellowfin tuna. In J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne, eds., *Marine Mammals and Fisheries*, pp. 238–252. Winchester, Md.: Allen and Unwin.

Ashmole, N. P. 1971. Seabird ecology and the marine environment. In D. S. Farner, D. R. King, and K. C. Parkes, eds., *Avian Biology*, 1:223–286. New York and London: Academic Press.

Ashmole, N. P. and M. J. Ashmole. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. *Peabody Mus. Nat. Hist., Yale Univ. Bull.* 24:1–131.

Au, D. W. K. and W. L. Perryman. 1982. Movement and speed of dolphin schools responding to an approaching ship. *U.S. Fish. Bull.* 80(2):371–379.

Au, D. W. K. and W. L. Perryman. 1985. Dolphin habitats in the eastern tropical Pacific. *U.S. Fish. Bull.* 83(4):623–643.

Au, D. W. K. and R. L. Pitman. 1986. Seabird interactions with dolphins and tuna in eastern tropical Pacific. *Condor* 88(3):304–317.

Barber, R. T. and F. P. Chavez. 1983. Biological consequences of El Niño. *Science* 222(4629):1203–1210.

Beverton, R. J. H. and S. J. Holt. 1959. A review of lifespan and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In G. E. W. Wolstenholme and M. O'Connor, eds., *The Lifespan of Animals, Ciba Foundation Colloquia on Aging,* 5:142–177. London: J. and A. Churchill.

Blackburn, M. 1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. *U.S. Fish. Bull.* 67:71–115.

Brandhorst, W. 1958. Thermocline topography, zooplankton standing crop, and mechanisms of fertilization in the eastern tropical Pacific. *J. Cons. Int. Explor.* Mer 24:16–31.

Calkins, T. P. 1975. Geographic distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics, 1971–1974. *Inter-American Tropical Tuna Comm., Bull.* 17:3–116.

Cole, L. C. 1949. The measurement of interspecies association. *Ecology* 30:411–424.

Charnov, E. L. 1976. Optimal feeding: the marginal value theorem. *Theor. Popul. Biol.* 9:129–136.

Clutton-Brock, T. H. and P. H. Harvey. 1977. Primate ecology and social organization. *J. Zool., London,* 183:1–39.

Cromwell, T. 1958. Thermocline topography, horizontal currents and "ridging" in the eastern tropical Pacific. *Inter.-Amer. Tropical Tuna Comm., Bull.* 3:135–164.

Crook, J. H. 1965. The adaptive significance of avian social organization. *Symp. Zool. Soc. London,* 14:181–218.

Crook, J. H. 1970. The socio-ecology of primates. In J. H. Crook, ed., *Social Behavior in Birds and Mammals,* pp. 103–166. London: Academic Press.

Diamond, A. W. 1983. Feeding overlap in some tropical and temperate seabird communities. In R. W. Schreiber, ed., *Tropical Seabird Biology,* pp. 24–46. Cooper Ornithological Society Studies in Avian Biology no. 8.

Fitch, J. E. and R. L. Brownell. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Bd. Canada* 25:2561–2674.

Gould, P. J. 1971. *Interactions of seabirds over the open ocean.* Ph.D. thesis. University of Arizona (Tucson).

Gould, P. J. 1974. Sooty Tern *(Sterna fuscata).* In W. B. King, ed., *Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean,* pp. 6–52. Smithsonian Contributions to Zoology, no. 158.

Hammond, P. S., ed. 1981. *Report on the workshop on tuna dolphin interactions, Managua, Nicaragua. Inter-American Trop. Tuna Comm.* Special Report no. 4.

Harrison, C. S., T. S. Hida, and M. P. Seki. 1983. Hawaiian seabird feeding ecology. *Wildl. Monogr.* no. 85.

Hewitt, R. P. and G. L. Friedrichsen. Manuscript. On birds and dolphins. Southwest Fisheries Center, La Jolla, Calif.

Hida, T. S. 1970. Surface tuna schools located and fished in equatorial eastern Pacific. *Comm. Fish. Rev.* 32(4):34–37.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54(2):427–432.

IATTC. 1984. *Annual Report of the Inter-American Tropical Tuna Commission* (IATTC), La Jolla, Calif. Table 1.

King, W. B. 1970. The trade wind zone oceanography pilot study, part 7: Observations of Seabirds, March 1964 to June 1965. Washington, D.C.: U.S. Fish and Wildlife Service, Special Scientific Report, Fisheries 586.

King, W. B., ed. 1974a. *Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean*, pp. 53–95. Smithsonian Contributions to Zoology, no. 158.

King, W. B. 1974b. Wedge-tailed Shearwater *(Puffinus pacificus)*. In W. B. King, ed., *Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean*, pp. 53–95. Smithsonian Contrib. to Zool. no. 158.

Leatherwood, S., D. K. Caldwell, and H. E. Winn. 1976. *Whales, Dolphins, and Porpoises of the Western North Atlantic.* NOAA Technical Report NMFS CIRC-396, National Marine Fisheries Service, Seattle, Wash.

Levenetz, J., A. Fonteneau, and R. Regalado. 1980. Resultats d'une enquete sur l'importance des dauphins dans la pecherie thoniere FISM. International Commission for the Conservation of Atlantic Tunas, Collective Volume of Scientific Papers 9(1):176–179.

Merle, J. 1978. *Atlas hydrologique saisonnier de l'ocean Atlantique intertropical.* Travaux et documents de l'Office de la Recherche Scientifique et Technique Outre-Mer, no. 82.

Miyazaki, N., T. Kasuya, and M. Nishiwaki. 1973. Food of *Stenella coeruleoalba*. *Sci. Rep. Whales Res. Inst.* 25:265–275.

Mullen, A. J. 1984. Autonomic tuning of a two predator, one prey system via commensalism. *Math. Biosciences* 72:71–81.

Murphy, G. I. and I. I. Ikehara. 1955. *A Summary of Sightings of Fish Schools and Bird Flocks and of Trolling in the Central Pacific.* Washington, D.C.: U.S. Fish and Wildlife Special Scientific Report, Fisheries 154.

Nelson, J. B. 1978. *The Sulidae: Gannets and Boobies.* Oxford: Oxford University Press.

Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *J. Anim. Ecol.* 46:511–529.

Olson, R. J. and C. H. Boggs. 1986. Apex predation by yellowfin tuna *(Thunnus albacares)*: Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Canad. J. Fish. Aquat. Sci.* 43(9):1760–1775.

Perrin, W. F., M. D. Scott, G. J. Walker, F. M. Ralston, and D. W. K. Au. 1983. *Distribution of Four Dolphins* (*Stenella* spp. and Delphinus delphis) *in the Eastern Tropical Pacific, with an Annotated Catalog of Data Sources.* National Marine Fisheries Service, La Jolla, California: National Oceanic and Atmospheric Administration Technical Memorandum NMFS-SWFC-38.

Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holts. 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. *U.S. Fish. Bull.* 71(4):1077–1092.

Philander, S. G. H. 1983. El Niño southern oscillation phenomena. *Nature* 302:295–301.

Pielou, E. C. 1969. *An Introduction to Mathematical Ecology.* New York and London: Wiley Interscience.

Pitman, R. L. 1986. *Atlas of Seabird Distribution and Relative Abundance in the*

*Eastern Tropical Pacific*. Southwest Fisheries Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Administrative Report LJ-86-02C.

Reintjes, J. W. and J. E. King. 1953. Food of the yellowfin tuna in the central Pacific. *U.S. Fish. Bull.* 54:91–110.

Robinson, B. H. and J. E. Craddock. 1983. Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei*. *U.S. Fish. Bull.* 81(2):283–289.

Safina, C. and J. Burger. 1985. Common tern foraging: seasonal trends in prey fish densities and competition with bluefish. *Ecology* 66(5):1457–1463.

Schoener, T. W. 1982. The controversy over interspecific competition. *Amer. Sci.* 70(6):516–595.

Schreiber, R. W. and E. A. Schreiber. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982–1983 perspective. *Science* 225(4663):713–716.

Sharp, G. D. 1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. In G. D. Sharp and A. E. Dizon, eds., *The Physiological Ecology of Tunas*, pp. 397–449. New York: Academic Press.

Sharp, G. D. and A. E. Dizon. 1978. *The Physiological Ecology of Tunas*. New York: Academic Press.

Smith, R. C., P. Dustan, D. Au, K. S. Baker, and E. A. Dunlop. 1986. Distribution of cetaceans and sea surface chlorophyll concentration in the California Current. *Marine Biology* 91(3):385–402.

Smith, T. D., ed. 1979. *Report of the Workshop on Status of Porpoise Stocks, La Jolla, Calif., August 27–31, 1979*. Southwest Fisheries Center, National Marine Fisheries Service, Administrative Report LJ-70-41.

Stretta, J. M. and M. Slepoukha. 1986. Analyse des facteurs biotiques et abiotiques associes aux bancs de thons. In P. E. K. Symons, P. M. Miyake, and G. T. Sakagawa, eds., *Proceedings, ICCAT Conference on the International Skipjack Year Program*, International Commission for the Conservation of Atlantic Tunas, pp. 161–169. Madrid: ICCAT.

Warren, C. E. and G. E. Davis. 1966. Laboratory studies on the feeding, bioenergetics, and growth of fish. In S. D. Gerking, ed., *The Biological Basis of Freshwater Fish Production*, pp. 175–214. Oxford and Edinburgh: Blackwell Scientific.

Wiens, J. A. 1984. Resource systems, populations, and communities. In P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, eds., *A New Ecology—Novel Approaches to Interactive Systems*, pp. 397–436. New York: Wiley.

Wyrtki, K. 1964. Upwelling in the Costa Rica Dome. *U.S. Fish. Bull.* 63:355–372.

Wyrtki, K. 1966. Oceanography of the eastern equatorial Pacific Ocean. *Oceanogr. Mar. Biol. Ann. Rev.* 4:36–68.

Appendix 5.1. Common and scientific names of species mentioned in text.

| | |
|---|---|
| TUNAS | |
| Yellowfin | *Thunnus albacares* |
| Bigeye | *T. obesus* |
| Skipjack | *Katsuwonus pelamis* |
| Frigate mackerel | *Auxis* spp. |
| BIRDS | |
| Boobies | |
| Red-footed | *Sula sula* |
| Masked | *S. dactylatra* |
| Brown | *S. leucogaster* |
| Wedge-tailed shearwater | *Puffinus pacificus* |
| Sooty tern | *Sterna fuscata* |
| Jaegers | *Stercorarius* spp. |
| Juan Fernandez petrel | *Pterodroma externa externa* |
| White-necked petrel | *Pterodroma externa cervicalis* |
| Dark-rumped petrel | *Pterodroma phaeopygia* |
| White tern | *Gygis alba* |
| Noddy terns | *Anous* spp. |
| Frigatebirds | *Fregata* spp. |
| Phalaropes | (Phalaropodidae) |
| Storm-petrels | (Hydrobatidae) |
| Gulls | *Larus* spp. |
| Tropic birds | *Phaethon* spp. |
| CETACEANS | |
| Delphinids | |
| Spotted dolphin | *Stenella attenuata* |
| Spinner dolphin | *S. longirostris* |
| Striped dolphin | *S. coeruleoalba* |
| Common dolphin | *Delphinus delphis* |
| Bottlenose dolphin | *Tursiops truncatus* |
| Risso's dolphin | *Grampus griseus* |
| Pilot whale | *Globicephala macrorhynchus* |
| Rough-toothed dolphin | *Steno bredanensis* |
| Melon-headed whale | *Peponocephala electra* |
| Fraser's dolphin | *Lagenodelphis hosei* |
| Pygmy killer whale | *Feresa attenuata* |
| False killer whale | *Pseudorca crassidens* |
| Killer whale | *Orcinus orca* |
| Dall's porpoise | *Phocoenoides dalli* |
| Whales | |
| Rorquals | |
| Blue | *Balaenoptera musculus* |
| Minke | *B. acutorostrata* |
| Sei | *B. borealis* |
| Bryde's | *B. edeni* |
| Ziphiids (beaked) | *Mesoplodon* spp.; *Ziphius cavirostris* |
| Sperm | *Physeter macrocephalus* |
| Dwarf/pygmy sperm | *Kogia* spp. |

5.3

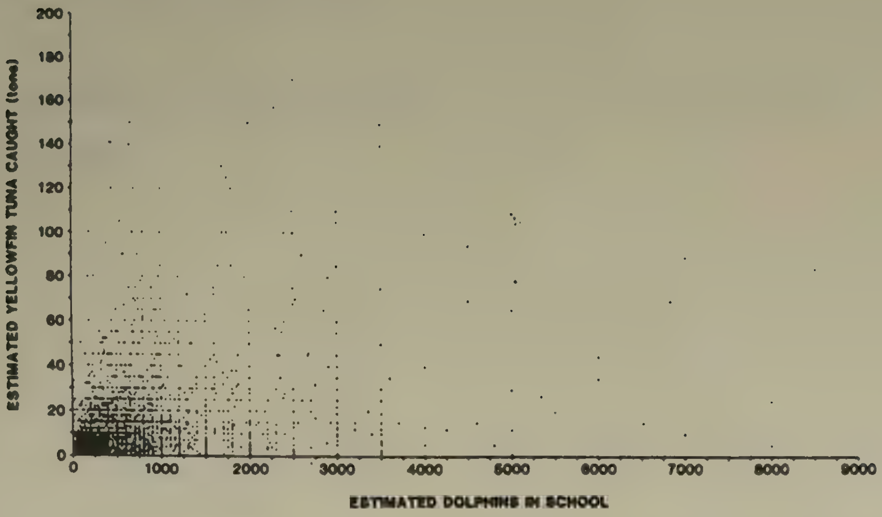
Appendix 5.2. Relationship between dolphin school size (numbers) and the catch (in short tons) of associated yellowfin tuna. Data collected by SWFC observers abroad U.S. purse seiners, 1981 through 1985.

| | COAST–110°W LONGITUDE | | | | | | 110°W–140°W LONGITUDE | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Porpoise fish[a] | | School fish[b] | | All | | Porpoise fish[a] | | School fish[b] | | All | |
| YEAR | n | (%) | n | (%) | n | (%) | n | (%) | n | (%) | n | (%) |
| 5°N–25°N Latitude | | | | | | | | | | | | |
| 1981 | 374 | (97.6) | 102 | (79.4) | 476 | (93.7) | 328 | (95.7) | 78 | (24.4) | 406 | (82.0) |
| 1982 | 378 | (98.4) | 67 | (80.6) | 445 | (95.7) | 179 | (96.6) | 74 | (33.8) | 253 | (78.3) |
| 1984 | 173 | (95.4) | 1 | (–) | 174 | (95.4) | 153 | (94.8) | 2 | (–) | 155 | (93.5) |
| 1985 | 728 | (93.0) | 24 | (–) | 752 | (91.8) | 157 | (99.4) | 0 | (–) | 157 | (99.4) |
| 1981–85 | 1,653 | (95.5) | 194 | (76.8) | 1,847 | (93.6) | 817 | (96.4) | 154 | (28.6) | 971 | (85.7) |
| 5°N–15°S Latitude | | | | | | | | | | | | |
| 1981 | 44 | (75.0) | 122 | (33.6) | 166 | (44.6) | 43 | (81.4) | 0 | (–) | 43 | (81.4) |
| 1982 | 166 | (87.4) | 55 | (38.2) | 221 | (75.1) | 68 | (83.8) | 4 | (–) | 72 | (83.3) |
| 1984 | 27 | (92.6) | 0 | (–) | 27 | (92.6) | 1 | (–) | 0 | (–) | 1 | (–) |
| 1985 | 11 | (–) | 0 | (–) | 11 | (–) | 0 | (–) | 0 | (–) | 0 | (–) |
| 1981–85 | 248 | (86.3) | 177 | (35.0) | 425 | (64.8) | 112 | (83.0) | 4 | (–) | 116 | (82.8) |

NOTES: These 1981–85 data are of sets (= purse seine launches) during a period straddling the 1982–83 El Niño event and during which time fishermen have often checked tuna schools for size before setting on the school. The data were collected by SWFC technicians aboard U.S. purse seiners. % = percentage of *n* tuna school set upon by the seiners that were with birds. (–) indicates unreliable percentage because of small sample size. There is no data for 1983.

[a] "Porpoise fish" = tuna schools associated with dolphins.

[b] "School fish" = not associated with dolphins.



**Appendix 5.3.** The percent of yellowfin tuna schools (n) (set upon by purse seiners) that were with birds, according to area and whether schools were with dolphins ("porpoise fish") or not ("school fish").

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David W. Au, Michael D. Scott, and Wayne L. Perryman

# LEAP-SWIM BEHAVIOR OF "PORPOISING" DOLPHINS

## ABSTRACT

*Dolphins leap or "porpoise" when swimming fast. Hypothetically, there is a "crossover" speed, above which leaping is energy saving. Field measurements indicate this speed is near 3.5 m/s. Observations also show that when moving at high speed, dolphins can continue to swim long distances under water, a behavior that current models of leaping-swimming behavior had not predicted.*

A school of leaping dolphins that is literally churning the sea to froth obviously utilizes (and wastes) considerable energy, though we now know that these mammals possess no special mechanisms of power utilization (Hui 1987). It is also obvious that at high swimming speeds, dolphins find leaping advantageous, whatever the energy costs. Au and Weihs (1980) explained this by introducing the concept of "crossover" speed, above which dolphins should actually save energy by leaping. Their model and equation for this speed was based on an idea, first proposed by Hertel (1966), that leaping can be a way for fast-swimming animals to escape the increased drag encountered in the near-surface layer due to the animals' generation of surface waves. Recently, Blake (1983) discussed crossover speeds for a variety of aquatic animals after deriving a relationship that simplified to:

$$U_c = 18.47 \sqrt{L}$$

(where $U_c$ = the crossover speed in cm/s, and L = animal length in cm). This equation appeared in some respects to be more realistic than that of Au and Weihs because it took into account the effects of propulsive body oscillations in addition to the previously considered, simple energetics of leaping vs. swimming. A typical 200-cm dolphin would accordingly have a $U_c$ of 2.61 m/s or 5.1 knots (1 m/s = 1.94 knots).

Nevertheless, certain field observations of swimming and porpoising dolphins indicate that the crossover speed of a typical dolphin may be higher, though perhaps not as high as the 5 m/s (9.7 knots) predicted by Au and Weihs. Table 1 summarizes swimming speeds of dolphins (*Stenella spp.*) measured by Au and Perryman (1982) that, for the most part, appeared to be swimming at below crossover speeds. These dolphins, it was noted, broke the surface with little commotion and swam relatively long distances between leaps, even at speeds of 3.6-4.6 m/s (although "splash-leaping" was observed once at 3.4 m/s and at 5.2 m/s). Their mean speed was 3.5 m/s:

Table 1. Speeds of swimming dolphins (*Stenella* spp.) in meters per second.

| School | No. of Speed Measurements | Mean Speed (m/s) | Speed Range (m/s) |
|---|---|---|---|
| 1 | 7 | 3.1 | 2.1 - 4.3 |
| 2 | 11 | 3.0 | 2.2 - 4.3 |
| 3 | 11 | 3.7 | 2.5 - 6.7 |
| 4 | 6 | 2.6 | 1.5 - 3.4 |
| 5 | 5 | 4.5 | 1.3 - 4.8 |
| 6 | 7 | 4.4 | 3.6 - 5.2 |
| 7 | 6 | 3.7 | 1.3 - 5.9 |

These speeds were calculated from the relative distances and motions of schools with respect to the observation ship. The field notes describe these dolphins as mostly "swimming smoothly" (Au & Perryman 1982).

The long swimming distances between leaps is significant because Au and Weihs implied, in their derivation of crossover speed, that dolphins moving faster than this speed should swim short distances underwater between leaps, both to minimize their time in the impeding water medium and to accommodate a higher respiration rate. This seemed to be supported by shipboard observations, but that impression may need reconsideration. Figure 1 is a schematic of how they viewed dolphin locomotion at different speeds.

Described here will be some recent observations of dolphin swimming behavior that bear on these ideas.

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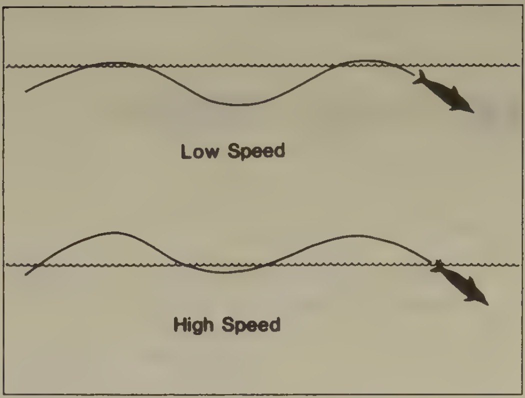

Figure 1. Schematic model of porpoising behavior.

The data to be presented come from examination of an aerial photograph of spotted dolphins (*Stenella attenuata*) leaping at high speed.

## DATA AND RESULTS

Scott et al. (1985) and Scott and Perryman (in press) took vertical aerial photographs of dolphin schools off southwestern Mexico using a 127 mm (5 in.) film size reconnaissance camera. We found one photograph (Figure 2) to be particularly useful because it showed several sequences of leaping-swimming behavior, each indicated by a series of splash remnants trailing behind a dolphin. The photograph was taken from an altitude of 247 m (810 ft). The dolphins then had been moving rapidly ("running") probably for less than two minutes. With close inspection, the animals can be seen along the perimeter of the splashes or splash remnants.

Each completed leap within a leap-swim sequence leaves a characteristic splash remnant, which consists of white water on the sea surface in the shape of a lengthwise cut mushroom. The actual exit splash creates the mushroom "stem" of the splash remnant from water carried out and then shed by the leaping animal. The actual re-entry splash creates the mushroom "cap" of the remnant, apparently from water whose modified trajectories originate from both antero-lateral sectors of the actual splash, which is cone-shaped and inclined backwards. We define the leap length as the distance between centers of the exit and re-entry splash remnants. Similarly, swimming length is the distance between centers of the re-entry and exit splash remnants.

Actual lengths of animals (in meters) and of distances between sequential splash remnants (in body lengths and in body lengths converted to meters) were calculated from the photograph using the basic photogrammetric formula (Thompson 1966):

$$L = (H/f)\ i$$

(where L = actual length, H = altitude of the photographing aircraft, f = focal length of the camera, and i = image length of the animal or of the splash (or remnant) interval on the photograph). We carefully measured the image lengths

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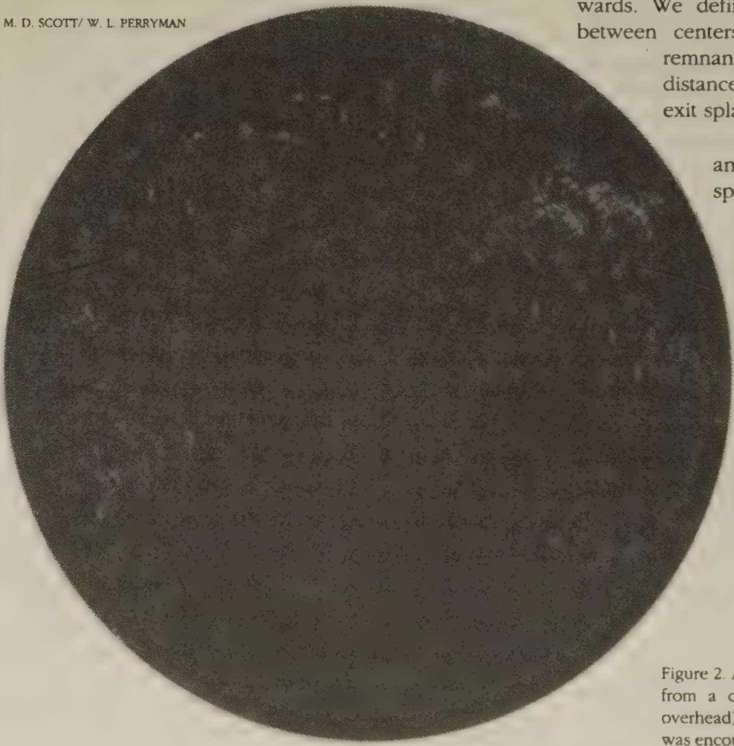

Figure 2. Aerial photograph of spotted dolphins scattering from a disturbance (presumably the airplane directly overhead). This school, estimated to contain 300 dolphins, was encountered in the eastern tropical Pacific off Mexico.

on the film to the nearest 0.025 millimeter using a calibrated stage micrometer on a 3X-power dissecting microscope. The precision of and bias in such calculated lengths and distances involves several considerations and is discussed by Hammond et al. (MS), and Scott and Perryman (in press). In their work, they found that the coefficient of variation of multiple measurements on individual dolphin images varied from 0.5-1.6 percent.

These lengths and distances in turn enabled the calculation of swimming speeds from the simple ballistic equation:

$$U = \sqrt{Rg/\sin 2\Theta}$$

(where U = swimming speed at leap exit in m/s, R = leap length in m, $g = 9.8\ m/s^2$, and Θ = launch angle).

The average leap length was an impressive 6.8 m (Table 2). From it we calculated the mean horizontal speed of the dolphins to be 8.2 m/s, using the above equation and assuming a ballistic trajectory with 45° launch angle. (Reducing the average leap length by two standard errors would give 7.7 m/s; angles other than 45° would give higher speeds.) Between leaps, the dolphins were often clearly visible; frequently, they appeared to be swimming less than 2 m under the surface with little change of depth.

Interestingly, the splash remnant patterns show that swim lengths were greater (on average, 1.9 times greater) than leap lengths (Table 2). (This ratio should be little affected by errors.) This finding is contrary to the model for high speed swimming shown in Figure 1-B. Thus, these dolphins swam long distances even when traveling above crossover speed.

## DISCUSSION

It is possible to show that the crossover speed of a 200-cm dolphin can be 3.4 m/s, or even 6.3 m/s, if it is assumed that the dolphin swims below the high-drag surface layer between leaps and that the leap actually begins and ends beneath the sea surface, or if certain other assumptions are made regarding the mass of water carried out by the leaping animal. These variants of the crossover speed equation would accommodate some of the ideas of Gordon (1980). But all such calculations merely show that moderate adjustments in multi-parameter equations lead to a range of results. We are not confident that these equations are realistic.

We have not been able to determine crossover speed empirically and can only suggest its approximate value. Part of the reason is that it is unclear how to recognize this speed when it occurs. Are dolphins that are porpoising gently, with their bodies barely clearing the water, actually leaping or even in the leaping mode? The dolphins described in Table 1 appeared to be porpoising gently at 3.5 m/s on average (6.8 knots); long, splashing leaps were seldom seen. In contrast, the dolphins in Figure 2 were clearly above crossover speed; their long leaps and large exit and re-entry splashes exemplified that spectacular locomotory behavior that so strongly imparts the impression of power in these animals. Their average speed was calculated at 8.2 m/s (15.9 knots). Such speeds are not sustainable, for elsewhere when we have pursued dolphins of the genus *Stenella* with a ship traveling at 5.2 m/s, those dolphins (which would often break into the leaping mode) still could not escape except by scattering. These observations suggest that the crossover speed lies below 8.2 m/s and is near 3.5 m/s.

**Table 2. Means of size, leap length, and swim length of individuals from a school of "running" spotted dolphins (*Stenella attenuata*).**

| | n | $\bar{x}$ | st. dev. |
|---|---|---|---|
| Animal length | 19 | 1.71 m | 0.21 m |
| Leap length | | | |
| in body lengths | 26 | 3.96 | 1.11 |
| in meters | 26 | 6.77 m | 1.90 m |
| Swim length | | | |
| in body lengths | 9 | 7.45 | 1.01 |
| in meters | 9 | 12.74 m | 1.73 m |

Animal length measurements tend to be underestimates because of the difficulty in discerning the exact limits of body size from the photograph (see Figure 2) due in part to slight flexing of the body. Twenty animals were tracked and measured. One calf was eliminated from the calculation of mean length. From 0-2 swim lengths and 1-3 leap lengths could be measured for each animal.

It was surprising that the fast-moving dolphins of Figure 2 swam underwater an average distance almost double the leap length, for we thought that the high-speed, leap-swim sequence should at least be symmetrical with respect to the sea surface, if not like that of Figure 1-B. Why should these dolphins swim so long underwater when leaping was already clearly advantageous? Their speed should have induced frequent leaping, even if swimming were well below the high-drag surface layer. It is possible that they accelerated to leap, that between leaps they were swimming more slowly than when they were leaping. But, if so, it is unclear why that would be advantageous in-flight behavior. Perhaps the dolphins were using a variant of the energy-saving, two-phase power and glide swimming (Weihs 1974), where the glide phase begins at the top of the leap. Hui (1986) photographed penguins of the genus *Spheniscus* leaping and swimming at a mean speed of 3.7 m/s, which was above the empirically determined speed of 3.0 m/s at which they regularly began leaping. The birds' swim lengths averaged 3.6 times their leap lengths, an even larger factor than measured for the dolphins in Figure 2. He also noted the discrepancy with previous models of leaping and suggested that breathing rate and time required for inhalation, rather than swimming speed alone, might control porpoising behavior. That would be consistent with the observations since neither the dolphins nor the penguins were likely very tired or breathing rapidly when photographed. At faster breathing rates, swim lengths may very well decrease, while leap lengths may change little.

The long swim lengths, apparently at speeds that should induce leaping, remain an enigma of our present understanding, which is admittedly rudimentary. But however complex leap-swim behavior may actually be, the principle of energy efficiency and conservation is probably maintained. Even the great splashes that accompany leaping probably represent a compromise between the energetic needs of streamlined, underwater propulsion and the requirements for smooth exit and reentry through the water surface

Certainly there is more to be learned. Why, for example, is it advantageous for some species of dolphins to bunch tightly when porpoising while, for some others, porpoising in lines abreast appears characteristic? And why do leaping dolphins re-enter the water with their pectoral fins extended?

## Literature Cited

Au, D., & Weihs, D.
1980 At high speeds dolphins save energy by leaping. *Nature* **284**:548-550.

Au, D , & Perryman, W.
1982 Movement and speed of dolphin schools responding to an approaching ship. *Fishery Bulletin, United States* **80**:371-379.

Blake, R. W.
1983 Energetics of leaping in dolphins and other aquatic animals. *Journal of the Marine Biological Association of the United Kingdom* **63**:61-70.

Gordon, C. N.
1980 Leaping dolphins. *Nature* **287**:759.

Hammond, P. S.; Scott, M. D.; & Perryman, W. L.
(MS) Obtaining lengths from photographs. Located at: Inter-American Tropical Tuna Commission, La Jolla, California.

Hertel, H.
1966 *Structure, Form and Movement.* Reinhold, New York.

Hui, C. A.
1986 The porpoising of penguins: an energy-conserving behavior for respiratory ventilation? *Canadian Journal of Zoology* **65**:209-211.

Hui, C. A.
1987 Power and speed of swimming dolphins. *Journal of Mammalogy* **68**(1):126-132.

Scott, M. D.; Perryman, W. L.; & Clark, W. G.
1985 The use of aerial photographs for estimating school sizes of cetaceans. *Bulletin, Inter-American Tropical Tuna Commission* **18**(5):383-419.

Scott, M. D., & Perryman, W. L.
In press Using aerial photogrammetry to study dolphin school structure. Pryor, K., & Norris, K. S., editors: School Structure *and Social Behavior of Wild Delphinids.* University of California Press, Los Angeles.

Thompson, M. M.
1966 Editor-in-chief, *Manual of Photogrammetry.* American Society of Photogrammetry, Falls Church, Virginia, Chapter 2.

Weihs, D.
1974 Energetic advantages of burst swimming of fish. *Journal of Theoretical Biology* **48**:215-229.

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# HEMATOLOGY AND SERUM CHEMISTRY OF THE YOUNG HAWAIIAN MONK SEAL (*MONACHUS SCHAUINSLANDI*)

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ABSTRACT: Between January 1984 and May 1987, blood samples were collected from 12 young (3- to 6-mo-old) Hawaiian monk seals (*Monachus schauinslandi*) that were captured in the wild and held in captivity. All samples evaluated were from clinically normal animals. Average hematologic and serum chemistry values were not remarkable for a young diving mammal. The blood and serum analyses performed established reference ranges, which can be used as indicators of health status for this endangered species.

*Key words:* Hawaiian monk seal, *Monachus schauinslandi*, hematology, serum chemistry, reference ranges.

## INTRODUCTION

The breeding range of the endangered Hawaiian monk seal (*Monachus schauinslandi*) is limited to the northwestern Hawaiian Islands, from Nihoa Island to Kure Atoll in the Hawaiian Archipelago. In the past, human disturbance has been responsible for significant population declines (Kenyon and Rice, 1959; Rice, 1960; Johnson et al., 1982). Other environmental factors also may limit the size of the population: shark predation (Taylor and Naftel, 1978; Balazs and Whittow, 1979; Alcorn and Kam, 1986), natural toxins (Gilmartin et al., 1980), injury of adult females and immature seals of both sexes from mobbing by adult male seals (Johnson and Johnson, 1981; Alcorn, 1984), entanglement in debris (Henderson, 1984), and food availability (Kenyon, 1973). Total seal beach counts over the breeding range have been reduced to <50% of the counts observed in the late 1950's.

Research activities to assist recovery of the Hawaiian monk seal population currently involve the use of animals held in temporary and permanent captivity. Reference ranges for normal hematologic and serum chemistry values are needed for routine clinical evaluation of all captive animals. For young animals in temporary captivity, indices are useful also as part of a screening program (performed prior to release), which protects against the potential transfer of disease between island populations.

## MATERIALS AND METHODS

### General methods

In 1984–1987, 12 recently weaned Hawaiian monk seals were collected from the northwestern Hawaiian Islands for various research activities in Honolulu. Hematology and serum chemistry analyses were performed on each animal at least once while between 3 and 6 mo of age.

In captivity, the young seals were fed a diet of frozen herring and smelt at 5–8% of their body weight and were supplemented with multivitamins, thiamine, and vitamin E. They were housed in enclosures that allowed swimming and haul-out activities.

Animals were not anesthetized for samplings and were manually restrained. Efforts were made to minimize the stress of handling, and seals were cooled with water throughout the procedures. An 18-gauge, 7.6-cm spinal needle and multiple 35-cc plastic syringes were used to draw 60–70 cc of whole blood from the extradural vein in the caudal lumbar area as described in Geraci and Smith (1975). Silicone-treated glass collection tubes were used for serum collection, and tubes containing ethylenediaminetetraacetic acid disodium salt (Na-EDTA) were used for hemogram studies. Fresh blood smears were prepared on glass slides for differential counts of white blood cells. All samples were centrifuged and separated within 1 hr of collection. Serum samples were refrigerated between the time of blood separation and serum analysis.

In Hawaii, available laboratory resources for blood analyses are limited to automated techniques that are set to human standards. Delivery of samples to a marine mammal reference laboratory requires a minimum of 2 days transit time and is impractical for the clinical purposes of the Hawaiian monk seal program on Oahu. All hematology and serum chemistry analyses used in computations of reference ranges were performed by Accupath, a SmithKline Bioscience Laboratory (Honolulu, Hawaii 96822, USA). Coulter 4C hematology reference control (Coulter Electronics, Inc., Hialeah, Florida 33010, USA) was used for all hematological determinations, including white blood cell count (WBC), red blood cell count (RBC), hemoglobin (Hgb), hematocrit (Hct), and mean corpuscular hemoglobin concentration (MCHC). At least 100 leukocytes were counted to determine differential cell counts on Wright-Giemsa-stained smears.

Blood chemistry tests performed on the Boehringer Mannheim Diagnostics 8600R analyzer (Boehringer Mannheim Diagnostics Division, 9115 Hague Road, Indianapolis, Indiana 46250, USA) and respective methods included total protein, Biuret; albumin, Bromcresol green; glucose, hexokinase; blood urea nitrogen, UV endpoint; creatinine, Jaffe; uric acid, uricase; bilirubin, Jendrassik-Groff (modified); cholesterol, enzymatic; triglycerides, enzymatic; alkaline phosphatase, alpha-napthyl phosphate; aspartate aminotransferase and alanine aminotransferase, IFCC; lactate dehydrogenase, Wacker (modified); gamma glutamyl transferase, Szasz + Persign; sodium and potassium, flame photometry; chloride, Schoenfeld + Lewellen (modified); calcium, Cresophthalein compexone; and phosphorous, Phosphomolybdate. Globulin values were calculated by subtracting albumin from total protein.

The data sets for each of the hematologic and serum chemistry parameters were examined for normal distribution by the Shapiro-Wilk statistic (SAS Institute Inc., 1985). The mean ($\bar{x}$), median, and standard deviation (SD) were determined by Grubbs $T$-statistic (Grubbs, 1969; Lumsden and Mullen, 1978). Statistics reported for data sets were then recalculated with "outliers" removed.

### Verification of laboratory methods

As is well known, differences in analytical equipment and methodologies as well as use of differing reference standards can lead to variable results between analytical laboratories (International Symposium on Quality Control 1979; Hector, 1986; Blijenberg et al., 1987). To establish the validity of measured values as determined by the local human reference laboratory (Accupath) in relation to those that might be determined at a facility with machines standardized for pinniped studies, four sets of whole blood and serum samples were split for duplicate analyses by Accupath and the Animal Care Laboratory at Sea World (San Diego, California 92109, USA). Both whole blood and serum analyses were performed at Accupath on the day of animal sampling and again on the date of evaluation by the Animal Care Laboratory.

Sodium heparin has been shown to be the anticoagulant most effective at stabilizing whole blood during long storage (Geraci and Engelhardt, 1974). Whole blood stored in EDTA at 4 C for 2 days should not be significantly altered by time-related changes (Geraci and Engelhardt, 1974). To insure that the type of anticoagulant used was not a limiting factor, the hemogram samples sent to Sea World for analysis were again split for storage in both sodium heparin and EDTA. Differences between paired whole blood and serum samples were evaluated by a two-tailed Student's $t$-test (Weissberg and Beatty, 1960).

## RESULTS

Hematologic and serum chemistry data are summarized and presented in Tables 1 and 2. Data sets were normally distributed for all but two parameters, basophils and band neutrophils (skewness: bands, 2.08; basophils, 2.45). Of 16 white blood cell differential counts, only four animals exhibited band neutrophils (5%, 4%, 2%, 1%), and only two animals, basophils (1%, 1%). These two parameters were not treated for outliers because of skew.

No outliers were found among the other individual hematologic measurements. Among the serum chemistry values, only one outlier was found and was excluded from statistical determinations: alkaline phosphatase was elevated in one seal at 521 U/liter. There were no apparent indications of a pathologic or iatrogenic cause for elevated alkaline phosphatase in this animal.

For the test of validation of hematologic data, the paired blood samples analyzed at the Sea World laboratory did not differ significantly ($P = 0.05$) from those values reported by Accupath. Neither were there

TABLE 1. Hematologic values of the Hawaiian monk seals.[a]

| Hematologic parameter[b] | n | Range | Mean | Median | SD | $\bar{x}$ ± 2 SD |
|---|---|---|---|---|---|---|
| WBC (× $10^3/\mu l$) | 16 | 5.7–11.2 | 8.8 | 8.9 | 1.6 | 5.6–12.0 |
| Segmented neutrophils (%) | 16 | 2.9–6.05 | 4.3 | 4.4 | 1.0 | 2.3–6.3 |
| Bands (%) | 16 | 0–0.5 | 0.1 | 0 | 0.2 | 0–0.41 |
| Lymphocytes (%) | 16 | 1.7–4.6 | 3.6 | 3.7 | 0.9 | 1.8–5.4 |
| Monocytes (%) | 16 | 0.2–1.1 | 0.5 | 0.5 | 0.3 | 0–1.1 |
| Eosinophils (%) | 16 | 0–0.6 | 0.2 | 0.2 | 0.2 | 0–0.5 |
| Basophils (%) | 16 | 0–0.1 | 0 | 0 | 0 | 0–<0.1 |
| RBC (× $10^6/\mu l$) | 15 | 3.1–4.3 | 3.6 | 3.7 | 0.3 | 3.0–4.2 |
| Hgb (g/dl) | 15 | 14.5–21.8 | 18.5 | 18.5 | 1.7 | 15.1–21.9 |
| Hct (%) | 15 | 44.2–61.3 | 54.7 | 54.8 | 4.6 | 45.5–63.9 |
| MCV (fl) | 15 | 137.3–167.0 | 150.7 | 150.0 | 7.6 | 135.5–165.9 |
| MCH (pg) | 15 | 47.1–54.4 | 50.9 | 50.9 | 2.2 | 46.5–55.3 |
| MCHC (g/dl) | 15 | 32.6–35.5 | 33.7 | 33.8 | 0.7 | 32.3–35.1 |

[a] Analysis performed by Accupath Laboratory.

[b] Key: WBC = white blood cells, RBC = red blood cells, Hgb = hemoglobin, Hct = hematocrit, MCV = mean corpuscular volume, MCH = mean corpuscular hemoglobin, MCHC = mean corpuscular hemoglobin concentration.

differences between EDTA and heparin storage for the values of hematology samples evaluated at Sea World. Differences between most paired serum chemistry values also did not differ significantly ($P = 0.05$) between the two laboratories. The serum values for the enzyme lactate dehydrogenase and triglyceride were consistently different in all four paired serum samples. Evaluations of three other serum enzymes (alanine aminotransferase, aspartate aminotransferase, and gamma glutamyl transferase) differed significantly ($P = 0.05$) between laboratories.

TABLE 2. Serum chemistry values of young Hawaiian monk seals.[a]

| Parameter | n | Range | Mean | Median | SD | $\bar{x}$ ± 2 SD |
|---|---|---|---|---|---|---|
| Total protein (g/dl) | 20 | 5.8–8.1 | 7.0 | 7.1 | 0.6 | 5.8–8.32 |
| Albumin (g/dl) | 16 | 2.4–3.9 | 3.4 | 3.5 | 0.4 | 2.6–4.2 |
| Globulin (g/dl) | 16 | 3.0–4.5 | 3.6 | 3.5 | 0.5 | 2.6–4.6 |
| Glucose (mg/dl) | 16 | 88–133 | 112.1 | 115 | 13.3 | 85.5–138.7 |
| Blood urea nitrogen (mg/dl) | 16 | 9–34 | 23.6 | 24.5 | 6.7 | 10.2–37.0 |
| Creatinine (mg/dl) | 16 | 0.5–1.7 | 1.0 | 1.1 | 0.3 | 0.4–1.6 |
| Uric acid (mg/dl) | 16 | 0.8–2.3 | 1.5 | 1.5 | 0.4 | 0.7–2.3 |
| Total bilirubin (mg/dl) | 16 | 0.2–0.5 | 0.3 | 0.3 | 0.1 | 0.1–0.5 |
| Direct bilirubin (mg/dl) | 16 | 0–0.1 | 0.07 | 0.10 | 0.05 | 0–0.17 |
| Cholesterol (mg/dl) | 16 | 187–568 | 317.3 | 303 | 98.4 | 120.5–514.1 |
| Triglycerides (mg/dl) | 16 | 28–91 | 55.4 | 49.5 | 17.3 | 20.8–90.0 |
| Alkaline phosphatase (U/liter) | 16 | 75–521 | 186.2 | 160.0 | 94.8 | 0–375.8 |
| Aspartate aminotransferase (U/liter) | 16 | 9–163 | 79.5 | 82.0 | 50.4 | 0–180.3 |
| Alanine aminotransferase (U/liter) | 16 | 13–148 | 58.5 | 34.0 | 47.4 | 0–153.3 |
| Lactate dehydrogenase (U/liter) | 16 | 442–1,544 | 832 | 792.5 | 305.4 | 221.2–1,442.8 |
| Gamma glutamyl transferase (U/liter) | 16 | 2–13 | 7.9 | 8.5 | 3.6 | 0.7–15.1 |
| Sodium (meq/liter) | 16 | 150–164 | 155 | 155 | 3.7 | 147.6–162.4 |
| Potassium (meq/liter) | 16 | 4.7–6.3 | 5.5 | 5.5 | 0.5 | 4.5–6.5 |
| Chloride (meq/liter) | 16 | 103–118 | 106.8 | 105 | 3.9 | 99.0–114.6 |
| Calcium (mg/dl) | 16 | 9.4–12.1 | 11.0 | 11.1 | 0.8 | 9.4–12.5 |
| Phosphorous (mg/dl) | 16 | 4.3–9.3 | 7.1 | 6.8 | 1.5 | 4.1–10.1 |

[a] Analysis performed by Accupath Laboratory.

## DISCUSSION

Hematologic adaptations to the aquatic lifestyle of pinnipeds have been examined by several investigators (Bryden and Lim, 1969; Lenfant et al., 1969, 1970; Ronald et al., 1969; Geraci, 1971; Greenwood et al., 1971; Lane et al., 1972; Wells, 1978; Wolk and Kosygin, 1979). Likewise, many comparative hematologic and/or serum chemistry studies between pinniped species have been presented (Lane et al., 1972; Hawkey, 1975; Engelhardt, 1979; Wolk and Kosygin, 1979; Needham et al., 1980). Although the hematologic and serum chemistry values of the young Hawaiian monk seal are not unexpected relative to other diving marine mammals, the purpose of this study is to present clinically useful information on the hematology and serum chemistry of this endangered species, rather than to discuss its physiology in relation to these values or to compare these values to those of other species.

Because of the constraints of dealing with an endangered pinniped species, the sample number is small, and only data collected from animals carefully judged to be clinically healthy are used in this report. Determinants of health status included historical condition, general appearance, activity level, feed intake around the day of sampling, and lack of recognizable disease indicators subsequent to sampling. The reported values are intended to serve as reference values for the clinical evaluation of animals and for recognition and analysis of disease states.

The effect of restraint on hematologic values was not determined. However, the hematologic changes that may occur with the stress response, including neutrophilia, monocytosis, lymphopenia, and eosinopenia (Geraci and Smith, 1975; Duncan and Prasse, 1981), were not notable in subsequent work in which samples were taken from healthy animals sedated by orally administered diazepam prior to venipuncture (Banish, unpubl. data).

Serum chemistry values can vary substantially for the same sample when analyzed by different equipment or methods or both (International Symposium on Quality Control, 1979; Hector, 1986). This is true especially for serum enzymes and was borne out by the paired serum sample analyses of this study. The only parameters in which reported values differed significantly between laboratories were four serum enzymes and triglycerides. Especially marked and consistent differences existed between the two laboratories in the evaluation of lactate dehydrogenase (LDH) and triglycerides. The results reported by the Sea World laboratory were 50% higher for LDH and 50% lower for triglycerides than those of the Accupath laboratory. The values for three other serum enzymes analyzed, including alanine aminotransferase (ALT), aspartate aminotransferase (AST), and gamma glutamyl transferase (GGT), were also disparate between the laboratories. In these cases, variations between paired samples were not consistent, but AST averaged 15% lower, ALT 27% lower, and GGT 50% lower at the Sea World facility than at the Accupath laboratory.

Laboratory methods at the Sea World laboratory included the use of Gilford analyses reagents (Ciba-Corning Diagnostics Corp., Gilford Systems, Oberland, Ohio 44074, USA). Triglycerides were evaluated by the Whlefeld method, LDH by the Wacker (modified), ALT and AST by I.F.F.C., and GGT by the Schasz procedure (modified). Despite the differences between laboratories, no values determined by the Sea World laboratory were beyond two standard deviations of the means (Table 2).

This information is clinically instructive in that it reiterates the need to establish a set of "normal" or reference values at a specific laboratory, and the value of using a consistent set of diagnostic laboratory methodologies when using blood data to evaluate any individual relative to a group of its species. At least small differences will likely exist between any two laboratories. Despite differences between the serum evaluations at the two laboratories in the test of paired serums, values as reported by this study for all parameters should be useful as indicators of the health status of an individual Hawaiian monk seal at any facility.

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## LITERATURE CITED

ALCORN, D. J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-42, 37 pp.

———, AND A. K. H. KAM. 1986. Fatal shark attack on a Hawaiian monk seal (*Monachus schauinslandi*). Marine Mammal Science 2: 313–315.

BALAZS, G. H., AND C. WHITTOW. 1979. First record of a tiger shark observed feeding on a Hawaiian monk seal. ʻElepaio 39: 107–109.

BLIJENBERG, B. G., H. A. ROETERING, AND B. LEIJNSE. 1987. Reflections on the standardization of total bilirubin in neonatal serum. Journal of Clinical Chemistry and Clinical Biochemistry 25: 177–181.

BRYDEN, M. M., AND G. H. K. LIM. 1969. Blood parameters of the southern elephant seal (*Mirounga leonina*, Linn.) in relation to diving. Comparative Biochemistry and Physiology 28: 139–148.

DUNCAN, J. R., AND K. W. PRASSE. 1981. Veterinary laboratory medicine—Clinical pathology. Iowa State University Press, Ames, Iowa, 243 pp.

ENGELHARDT, F. R. 1979. Haematology and plasma chemistry of captive pinnipeds and cetaceans. Aquatic Mammals 7: 11–26.

GERACI, J. R. 1971. Functional haematology of the harp seal *Pagophilus groenlandicus*. Physiological Zoology 44: 162–170.

———, AND F. R. ENGELHARDT. 1974. The effects of storage time, temperature, and anticoagulants on harp seal, *Phoca groenlandica*, hemograms: A simulated field study. Physiological Zoology 47: 22–28.

———, AND T. G. SMITH. 1975. Functional hematology of ringed seals (*Phoca hispida*) in the Canadian Arctic. Journal of the Fisheries Research Board of Canada 32: 2559–2564.

GILMARTIN, W. G., R. L. DELONG, A. W. SMITH, L. A. GRINER, AND M. D. DAILEY. 1980. An investigation into unusual mortality in the Hawaiian monk seal, *Monachus schauinslandi*. *In* Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, R. W. Grigg and R. T. Pfund (eds.). University of Hawaii Sea Grant College Program (UNIHI-SEAGRANT-MR-80-04), Honolulu, Hawaii, pp. 32–41.

GREENWOOD, A. G., S. H. RIDGWAY, AND R. J. HARRISON. 1971. Blood values in young gray seals. Journal of the American Veterinary Medical Association 159: 571–574.

GRUBBS, F. E. 1969. Procedures for detecting outlying observations in samples. Technometrics 11: 1–21.

HAWKEY, C. M. 1975. Comparative mammalian haematology: Cellular components and blood coagulation of captive wild animals. Heinemann Medical, London, England, 310 pp.

HECTOR, T. 1986. Assessment and control of biochemical methods, analytical chemistry by open learning. John Wiley & Sons, Chichester, England, 150 pp.

HENDERSON, J. R. 1984. Encounters of Hawaiian monk seals with fishing gear at Lisianski Island, 1982. U.S. National Marine Fisheries Service, Marine Fisheries Review 46: 59–61.

INTERNATIONAL SYMPOSIUM ON QUALITY CONTROL. 1979. The Third International Symposium on Quality Control, Excerpta Medica International Congress Series 483, Tokyo, Japan, 377 pp.

JOHNSON, A. M., R. L. DELONG, C. H. FISCUS, AND K. W. KENYON. 1982. Population status of the Hawaiian monk seal (*Monachus schauinslandi*), 1978. Journal of Mammalogy 63: 415–421.

JOHNSON, B. W., AND P. A. JOHNSON. 1981. The Hawaiian monk seal on Laysan Island: 1978. U.S. Department of Commerce, National Technical Information Services, Springfield, Virginia, PB-82-109661, 17 pp.

KENYON, K. W. 1973. Hawaiian monk seal (*Monachus schauinslandi*). *In* Seals, Proceedings of a Working Meeting of Seal Specialists on Threatened and Depleted Seals of the World. International Union for Conservation of Nature and Natural Resources New Series 39, Supplemental Paper 11, Morges, Switzerland, pp. 88–97.

———, AND D. W. RICE. 1959. Life history of the Hawaiian monk seal. Pacific Science 13: 215–252.

LANE, R. A. B., R. J. H. MORRIS, AND J. W. SHEEDY. 1972. A haematological study of the southern elephant seal, *Mirounga leonina* (Linn.). Comparative Biochemistry Physiology (A Comparative Physiology) 42A: 841–850.

LENFANT, C., R. ELSNER, G. L. KOOYMAN, AND C. M. DRABEK. 1969. Respiratory function of blood of the adult and fetus Weddell seal *Leptonychotes weddelli*. American Journal of Physiology 216: 1595–1597.

———, K. JOHANSEN, AND J. D. TORRANCE. 1970. Gas transport and oxygen storage capacity in some pinnipeds and the sea otter. Respiration Physiology 9: 277–286.

LUMSDEN, J. H., AND K. MULLEN. 1978. On establishing reference values. Canadian Journal of Comparative Medicine 42: 293–301.

NEEDHAM, D. J., C. F. CARGILL, AND D. SHERIFF. 1980. Haematology of the Australian sea lion, *Neophoca curerea*. Journal of Wildlife Diseases 16: 103–107.

RICE, D. W. 1960. Population dynamics of the Hawaiian monk seal. Journal of Mammalogy 41: 376–385.

RONALD, K., M. E. FOSTER, AND E. JOHNSON. 1969. The harp seal, *Pagophilus groenlandicus* (Erxleben, 1977). II. Physical blood properties. Canadian Journal of Zoology 47: 461–468.

SAS INSTITUTE INC. 1985. The univariate procedure. *In* SAS procedures guide for personal computers, 6th ed. Cary, North Carolina, pp. 343–357.

TAYLOR, L. R., AND G. NAFTEL. 1978. Preliminary investigations of shark predation on the Hawaiian monk seal at Pearl and Hermes Reef and French Frigate Shoals. Final report to U.S. Marine Mammal Commission, contract MM7AC011, NTIS PB-285 626, Washington, D.C., 34 pp.

WEISSBERG, A., AND G. H. BEATTY. 1960. Tables of tolerance-limit factors for normal distributions. Technometrics 2: 483–500.

WELLS, R. M. G. 1978. Observations on the haematology and oxygen transport of the New Zealand fur seal, *Arctocephalus forsteri*. New Zealand Journal of Zoology 5: 421–424.

WOLK, E., AND G. M. KOSYGIN. 1979. A hematological study of the walrus, *Odobenus rosmarus*. Acta Theriologica 24: 99–107.

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# HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: I. SHIP SURVEYS

Jay Barlow[1]

## ABSTRACT

The density and total population size of harbor porpoise along the coasts of California, Oregon, and Washington are estimated from ship surveys using line transect methods. Surveys were completed between September 1984 and May 1986 using teams of 3–5 observers. Data include 852 porpoise groups sighted during 6,590 km of transects. Sighting rates varied more due to effects of sea state than due to the presence of rain, fog, or sun glare. Experiments using additional observers indicate that approximately 22% of trackline groups were missed by a team of 5 observers. Harbor porpoise density is calculated from transects along the 18 m isobath and is extrapolated to other depth zones based on a model of porpoise abundance as a function of depth. Total population size is estimated as 45,713 (SE = 7,865) animals.

Approximately 200–300 harbor porpoise are taken annually in central California set net fisheries (Diamond and Hanan[2]; Hanan, et al.[3]). Little is known about porpoise abundance in this area. Dohl et al.[4] estimated that 1,600–3,000 porpoise reside in central and northern California based on their aerial surveys of coastal cetaceans. However, because harbor porpoise are frequently missed in aerial surveys (Kraus et al. 1983), this estimate is probably low. More information is needed on abundance, distribution, and population structure to determine the significance of harbor porpoise mortality in set nets.

Beginning in 1984, the National Marine Fisheries Service (NMFS) has conducted ship and aerial surveys of harbor porpoise abundance in California, Oregon, and Washington. This report presents results from four ship surveys. Results of the aerial surveys are presented by Barlow et al. (1988).

Porpoise density is estimated from survey data using line transect models (Burnham et al. 1980). Total abundance is estimated by extrapolating from density observed along transect lines to the entire area inhabited. Abundance in offshore regions is based on a model of porpoise density as a function of water depth. In addition to abundance estimation, survey data are used to examine the effect of environmental conditions on sighting efficiency and the possibility of temporal changes in harbor porpoise distribution.

## METHODS

### Ship Survey Methods

Surveys were conducted from two National Oceanic and Atmospheric Administration (NOAA) research vessels, the 52 m RV *David Starr Jordan* (Surveys 1, 3, and 4) and the 54 m RV *McArthur* (Survey 2)[5]. Both vessels were of similar design with viewing stations located on top of the pilothouse (viewing height was approximately 10 m above sea surface). Transect lines followed as close as possible to the 18 m isobath (roughly 2–4 km from the coast), although the actual depth along the transect varied from approximately 15–45 m, depending on the presence of local navigational hazards. The areas

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2] Diamond, S. L., and D. A. Hanan. 1986. An estimate of harbor porpoise mortality in California set net fisheries: April 1, 1983 through May 31, 1984. Adm. Rep. SWR-86-15, 40 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[3] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California net fisheries April 1, 1984 through March 31, 1985. Adm. Rep. SWR-86-16, 38 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[4] Dohl, T. P., R. C. Guess, M. L. Duman, R. C. Helm. 1983. Cetaceans of central and northern California, 1980–83: status, abundance, and distribution. Report prepared for U.S. Minerals Management Service, Contract #14-12-0001-29090, 284 p.

[5] Cruise reports available from the Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

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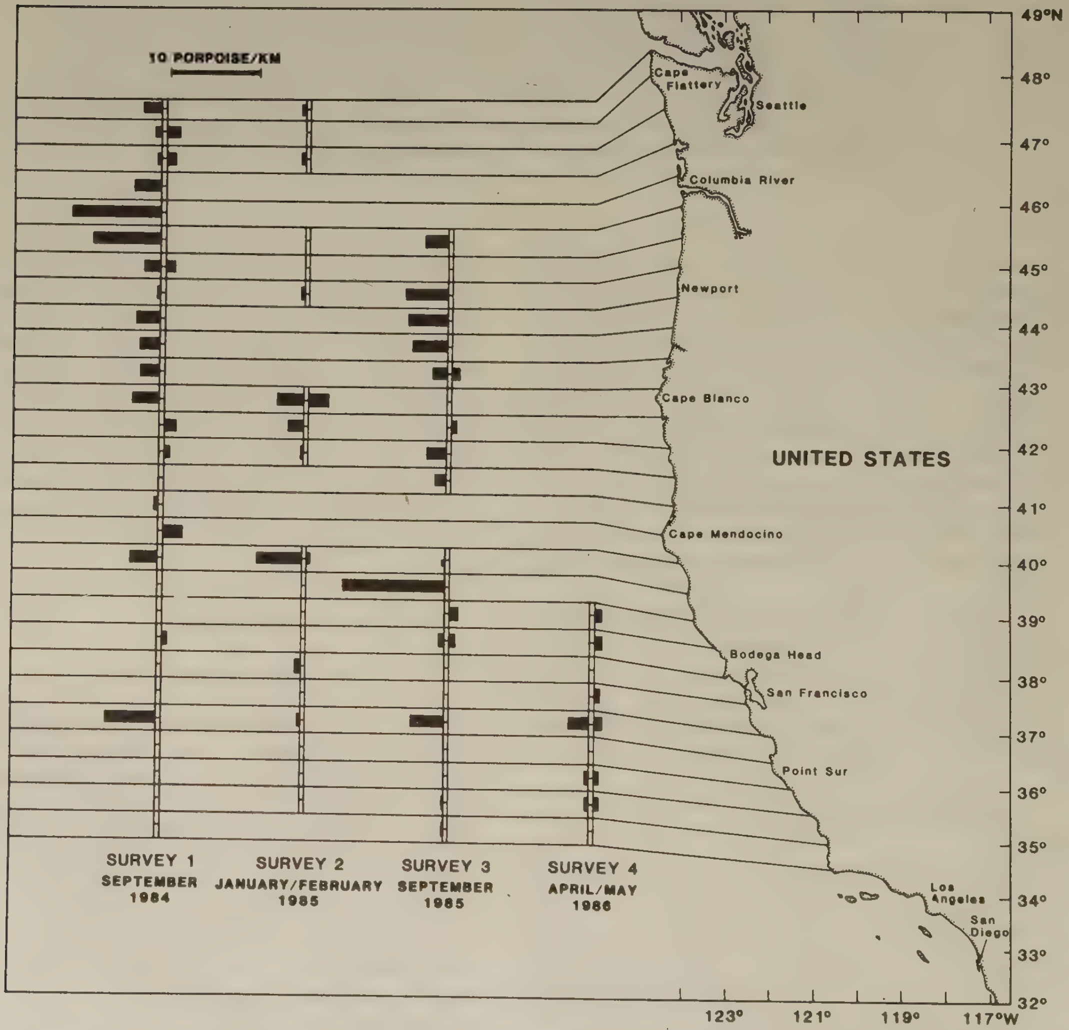
surveyed are shown in Figure 1. Survey design varied among the four trips:

*Surveys 1 and 3* were in September 1984 and 1985, respectively. Both were designed to survey harbor porpoise density and abundance from Point Conception, CA to Cape Flattery, WA. An attempt was made to survey the entire coastline on each of these cruises, but several sections of the coast were missed (Fig. 1) because of fog and heavy weather. Five observation positions were used on these two surveys.

*Survey 2* was from 24 January to 9 February 1985 and was primarily designed to examine seasonal changes in harbor porpoise distribution between Point Conception, CA and Cape Flattery, WA. Data from this cruise were not used for density or abundance estimation.


10 PORPOISE/KM
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Columbia River
Newport
Cape Blanco
UNITED STATES
Cape Mendocino
Bodega Head
San Francisco
Point Sur
Los Angeles
San Diego
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33°
32°
123°
121°
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117°W
SURVEY 1
SEPTEMBER
1984
SURVEY 2
JANUARY/FEBRUARY
1985
SURVEY 3
SEPTEMBER
1985
SURVEY 4
APRIL/MAY
1986

FIGURE 1.—Relative sightings per kilometer based on 30-minute latitudinal strata. Lines parallel to the coast indicate areas that were surveyed. Histograms indicate relative numbers of harbor porpoise seen per kilometer of transect, with bars to the left indicating relative numbers in calm seas (Beaufort 0, 1, and 2) and bars to the right indicating relative number in rough seas (Beaufort 3, 4, and 5).

*Survey 4* was from 24 April to 5 May 1986 and was designed to investigate factors which affect harbor porpoise density estimation. The surveys concentrated on several areas of high porpoise density in central California. The vessel's activities were coordinated with a helicopter to gather information on the avoidance of the ship by harbor porpoise. Experiments were also conducted on survey 4 to determine whether an independent team of 3 observers would sight any porpoise that were missed by the primary team of 5 observers. Data from this survey were not used for density or abundance estimation.

Typically, 8–10 observers were used on each survey, with a rested observer starting every half hour and rotating through 5 primary observation positions at half-hour intervals. The 5 positions consisted of port and starboard inboard observers, port and starboard outboard observers, and a recorder positioned amidship. The inboard observers searched with 7 power (7×) binoculars from straight ahead to 90° (survey 1) or to 45° (surveys 2, 3, and 4) on their respective sides of the vessel. On survey 1 the outboard observers searched with 25×, pedestal-mounted binoculars. Although sightings could be made at great distances from the vessel using the 25× binoculars, these distant sightings contributed little to the estimation of trackline density, and use of 25× binoculars was discontinued. On subsequent surveys, both the inboard and outboard observers used 7× binoculars. The outboard observers searched from straight ahead to 90° on their respective sides of the vessel. The recorder searched in the immediate vicinity of the ship using unaided eyes and (intermittently) 7× binoculars.

On survey 2, only 3 observation positions were used from Point Conception to Point Sur, CA and from Point Reyes, CA to Cape Flattery, WA. When effort was reduced to 3 observers, the inside observation positions were eliminated.

On survey 4, a second team of 3 observers was added to monitor the effectiveness of the principal team. This monitor team searched using unaided eyes and (intermittently) 7× binoculars from the pilothouse deck (viewing height approximately 7 m from sea surface). The principal team and the monitor team did not communicate sighting information, and independent records were kept.

Data were noted by the recorder on data coding forms. Data on search effort included the beginning and ending times and positions for continuous legs of effort, the ship's heading and speed, personal identification codes for the observers, sea surface temperature, water depth, Beaufort sea state, sun position relative to the ship, and codes indicating the presence of rain or fog within 5 km. The ship position was determined from a Loran navigational system or by triangulation using coastal landmarks and dead reckoning. Ship speed was recorded directly from the Omega/Loran system or was calculated based on time and distance traveled between successive position fixes along straight transect lines. Water depth was measured using a 38 kHz acoustic depth sounder.

Data for sightings consisted of the above elements, plus estimated group size, distance to shore, an estimate of the angle between the trackline of the ship and the group, and an estimate of the distance from the ship to the group. Group size refers to all the individuals associated with a sighting event. In most cases, groups were closely associated individuals that surfaced together (mean = 2.92, median = 2.0). In two cases (Point Arena and Monterey Bay, CA), groups consisted of 50–80 loosely associated individuals that were organized in subgroups of 4–10). Group size was estimated and recorded independently by each observer; the mean of these estimates was used in subsequent analyses. The angle from the trackline to the porpoise was estimated visually with the aid of a pelorus mounted in front of the observer stations, or, when 25× binoculars were used, from a calibrated collar on the pedestal mount. On surveys 1 and 2, distances to harbor porpoise were estimated visually using the radar distance-to-shore as a reference, or, when 25× binoculars were used, distances were estimated using calibrated reticles in the oculars. On surveys 3 and 4, distances were estimated using calibrated reticles in the oculars of 7× binoculars. Data were also collected on the porpoises' direction of travel relative to the ship.

The length of a transect was estimated as the product of ship speed and elapsed time. To stratify density estimates by sea state, rain, and fog, the effort record was divided into segments during which the sea state, rain, and fog codes did not change.

In five areas, information was collected on variation in harbor porpoise density with water depth. During survey 3, three sections of the coast were surveyed intensively (Fort Bragg to Cape Vizcaino, CA; Cape Blanco to Coquille Point, OR; and Cape Lookout to Tillamook Head, OR), with transect lines following the 18, 56, 92, and 185 m isobaths. On survey 4, the 18 and 46 m isobaths were surveyed in Monterey Bay, CA and in the vicinity of the Russian River, CA. These data formed the basis of a model (below) to extrapolate porpoise density from the usual transect lines (along the 18 m isobath) to deeper waters.

### Helicopter Observations

During survey 4, a Hughes 500-D helicopter was used to collect information on harbor porpoise behavior in response to the survey ship. The helicopter flew approximately 10 km ahead of the vessel, and 3 observers in the helicopter looked for harbor porpoise. Once a group of harbor porpoise was sighted, the helicopter hovered at 200–300 m while observers made behavioral observations and periodically recorded the helicopter's position using an on-board Loran system. Fluorescein dye packages were dropped in the water to allow the helicopter to maintain its position when harbor porpoise were diving. Radio communication was maintained with personnel on the ship who also kept records of the helicopter position using radar distances and bearings based on returns from an X-band radar transponder in the helicopter. The ship changed course, when necessary, to ensure that it passed in close proximity to the porpoise that were being observed. Porpoise observers on the ship were not aware of the helicopter's activities and were not told of sightings made by the helicopter observers (although they were able to see dye patches in some cases). Behavioral observations from the helicopter included time spent at the surface, time spent diving, and direction of porpoise movement.

### Density Estimation

Line transect methods were used to estimate the density of harbor porpoise from sightings. The assumptions of these methods are considered in detail in the discussion. The usual formula for estimating density ($D$) based on line transect surveys of small cetaceans is given by

$$D = \frac{f(0) \cdot n \cdot G}{2 \cdot L} \tag{1}$$

where $f(0)$ = the probability density function for sightings evaluated at zero perpendicular distance,
$n$ = number of sightings of groups,
$G$ = average group size calculated as the total number of individuals in all groups divided by the number of groups ($\Sigma N/n$), and
$L$ = length of the transect.

(Holt and Powers 1982; Hammond and Laake 1983; Holt in press). I did not use mean group size explicitly in abundance estimation, and density of harbor porpoise individuals, $D$, was estimated as

$$D = f(0) \cdot (R/2) \tag{2}$$

where $R$ = the number of individuals seen per length of transect ($\Sigma N/L$).

Equation (2) is functionally equivalent to Equation (1), but it simplifies variance estimation. Typically when using Equation (1), variances (and possibly covariances) must be estimated for $f(0)$, $G$, and $n$. Using Equation (2), variances are needed only for $f(0)$ and $R$, and covariance between mean group size and number of groups is handled implicitly. Sighting distributions appear to be independent of group size, $G$, (Results section), hence no adjustments were made to $f(0)$ for group size bias.

The parameter $f(0)$ is, in effect, a measure of sighting efficiency and should not vary with porpoise abundance. Sighting efficiency is, however, likely to change with sighting conditions, such as Beaufort sea state. Given these expectations and because relatively large sample sizes are needed to estimate $f(0)$ accurately, values for $f(0)$ were estimated for each survey by pooling all sightings within defined sea state categories. In order to estimate density on a finer scale, estimates of $R$ were stratified by geographic region and multiplied by the pooled estimate of $f(0)$.

The sighting probability density function evaluated at zero distance, $f(0)$, was determined empirically by fitting curves to the frequency distribution of sightings as a function of perpendicular distance from the trackline (Burnham and Anderson 1976). Differences in distributions of perpendicular distance were tested using the Kolmogorov-Smirnov 2-sample test. To avoid bias due to rounding error, angle and radial distance data were "smeared" (Butterworth 1982; Hammond and Laake 1983). Angles were smeared by adding a uniformly distributed random number between −5° and +5° to angle estimates. Radial distances were smeared by adding a uniformly distributed random number between 0.2 and +0.2 times the estimated distance. These smearing levels were based on the degree of rounding that was apparent from the data (Barlow[6]).

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[6] Barlow, J. 1987. Abundance estimation for harbor porpoise (*Phocoena phocoena*) based on ship surveys along the coasts of California, Oregon, and Washington. Adm. Rep. LJ-87-05.

Several models were investigated for estimating $f(0)$ from sighting distributions. The FORTRAN program Transect (Laake et al. 1979) was used to fit 2-, 3-, 4-, and 5-parameter Fourier series and 2-parameter exponential power series models. The FORTRAN programs Hazard and Hermite (S. Buckland[7]) were used to fit the 2-parameter hazard rate model (constrained such that parameter $P > 2$, Buckland 1985) and the 1-, 2-, 3-, and 4-parameter Hermite polynomial model (Buckland 1985). Of these models, the 2-parameter hazard rate model was selected based on its ability to fit the observed distributions and its lack of dependence on grouping criteria (Buckland 1985).

Perpendicular distances were grouped into strata, the size of which increased with perpendicular distance: 0–25 m, 25–50 m, 50–100 m, 100–200 m, 200–400 m, 400–800 m, 800–1,600 m, and 1,600–3,200 m. Several alternative groupings were investigated, and the choice of cutpoints made very little difference in estimates of $f(0)$. The above strata (increasing with distance) gave lower variances in $f(0)$ than when each stratum was of equal size (possibly because the hazard rate model assumes a distinct shoulder in the sighting distribution, and that shoulder is lost if the first distance strata are large).

No established criteria exist for choosing an appropriate perpendicular distance at which to truncate sighting distributions. Burnham et al. (1980) recommend that no more than 1–3% of sightings be eliminated by truncation. Using this recommendation, models were not able to adequately fit the observed sighting distributions. In this report, truncation distance was chosen in four ad hoc steps: 1) The hazard rate model was fit to perpendicular distance data truncated at distances of 400, 800, 1,600, and 3,200 m. 2) Truncation distances were identified which gave acceptable $\chi^2$ values ($P > 0.1$). 3) Of the acceptable truncation distances, the standard error in $f(0)$ was estimated empirically by randomly drawing 10 samples (of the same size as the original sample) from the observed distribution of perpendicular distances and by calculating the standard deviation of $f(0)$ estimated from each random sample. 4) Truncation distances were chosen as those which gave the lowest coefficient of variation in $f(0)$.

Variance in $R$, the number of porpoise seen per kilometer, was estimated using jackknife statistics (Efron 1982). Jackknife estimates were calculated by first estimating the value of $R$ using all data. The value, $R_k$, was again estimated excluding the $k$th segment of search effort. This process was repeated for each effort segment. To ensure that each $k$th segment was of equivalent length, effort segments with the same sea state, rain, and fog codes were combined in a linear array and were then divided into 10 segments of approximately equal length. The variance in the estimate of $R$ was calculated as

$$s^2 = \frac{9}{10} \cdot \sum_{k=1}^{10} (R_k - \bar{R})^2 \qquad (3)$$

The variance of $D$ was estimated using the Goodman (1960) product variance formula (assuming no covariance) using this jackknife variance for $R$ and the above Monte Carlo variance for $f(0)$.

### Fraction of Missed Animals

On survey 4, a second, independent team of 3 observers were used to estimate the fraction of harbor porpoise that are missed by the primary team of 5 observers. The fraction of missed animals in a sighting survey is analogous to the fraction of unmarked animals in a mark/recapture experiment (Pollock and Kendall 1987). This fraction was estimated using the Chapman (1951) modification of the Petersen (or Lincoln) index method (Pollock and Kendall 1987). Confidence limits were estimated using Adams' (1951) method, which assumes a binomial sampling distribution. Standard error was estimated using standard binomial formulas.

### Abundance Estimation

A model was used to estimate the number of harbor porpoise along the entire coastline based on the density that was observed along the 18 m isobath. In shallow areas, such as the Bering Sea and Georges Bank, harbor porpoise are found a considerable distance from land (Gaskin 1984), hence offshore distribution is better modelled as a function of depth than as a function of distance from shore. (Although harbor porpoise are also found in very deep water in fjords and inland waterways of Alaska [Taylor and Dawson 1984], this represents a special case that is not applicable to coastal waters considered here.) The model used to estimate abundance was based on data collected on surveys 3 and 4 and on data from a ship surveys by La Barr and

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Avail. from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[7] S. Buckland, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1986.

Ainley[8] and Szczepaniak[9] in central California. The number of harbor porpoise seen per kilometer of transect was taken as an index of relative density along each isobath. A simple descriptive model was then constructed to give relative density as a function of water depth.

Fifteen depth strata were used in abundance estimation: 0–10, 10–20, 20–30, . . ., and 140–150 m. The surface area within the strata was calculated from digitized bathymetric data. Kelp beds were assumed to be unsuitable as harbor porpoise habitat; hence, kelp bed area was subtracted from the total area within the 0–10 m stratum. Kelp bed areas for the entire west coast were taken from Crandall (1915). More recent estimates for limited areas in central California are in good agreement with these previous values (G. Van Blaricom[10]).

For each of 15 depth strata, the abundance of harbor porpoise was estimated as the product of their density along the survey line (the 18 m isobath), the density in that depth strata relative to that along the survey line, the surface area included within that depth strata, and the inverse of the estimated fraction of trackline animals that were seen. Since survey effort and harbor porpoise density both varied geographically, abundance estimates were made for each of 8 geographic regions (Fig. 2). Areas within the depth strata were estimated from NOAA bathymetric data. The estimate of total abundance along the coast, $N_T$, is therefore given by

$$N_T = \frac{1}{F} \cdot \sum_{j=1}^{8} D_j \sum_{k=1}^{15} (I_k \cdot A_{j,k}) \tag{4}$$

where $D_j$ = density of individuals observed on the transect line in the $j$th geographic strata,

$I_k$ = ratio of density in depth strata $k$ to that on transect line (see Figure 4),

$A_{j,k}$ = area in geographic region $j$ and depth strata $k$, and

$F$ = the estimated fraction of trackline animals seen by the usual team of 5 observers.

Equation (4) was applied independently to the different surveys and, within surveys, to different sea state strata. When combining estimates from different sea states or different cruises, abundance was calculated as the mean of the densities in each of the stratum, weighted by the length of the transect line within that stratum.

In estimating standard error for total abundance, variances of products were calculated using the Goodman (1960) product variance formula, and variances of ratios were estimated using a Taylor approximation (Yates 1953, p. 198). Area was assumed to be known without error. Statistical error in the indices of abundance for the depth strata could not be estimated given the paucity of available information. To account for uncertainty in the model of depth distribution, three versions of the model are proposed to span a range of possibilities.

## RESULTS

On the four surveys, 852 groups of harbor porpoise were sighted (an estimated 1,818 individuals). A distance of 6,590 km was surveyed during 56 days. The number of sightings per kilometer surveyed varied geographically and these geographic patterns appeared to change appreciably between cruises (Fig. 1).

### Sighting Distributions

The number of sightings on the inshore and offshore sides of the vessels were approximately equivalent (383 and 392, respectively). The cumulative distributions of perpendicular sighting distances were not significantly different for these two sides ($P = 0.06$). Therefore, sighting distributions were assumed to be symmetrically distributed about the trackline, and the distributions of perpendicular sighting distances from both sides of the vessel were pooled for subsequent analyses.

The distributions of perpendicular sighting distances for the first three surveys were significantly different from one another ($P < 0.01$ for all). This was probably the result of the modifications in survey methods between these cruises. Surveys 3 and 4 used the same methods, and sighting distributions were not significantly different ($P = 0.39$). Given that changes in methods result in differences in sighting distributions, all surveys were treated separately in subsequent analyses.

Distributions of perpendicular distance were not significantly different between individuals sighted

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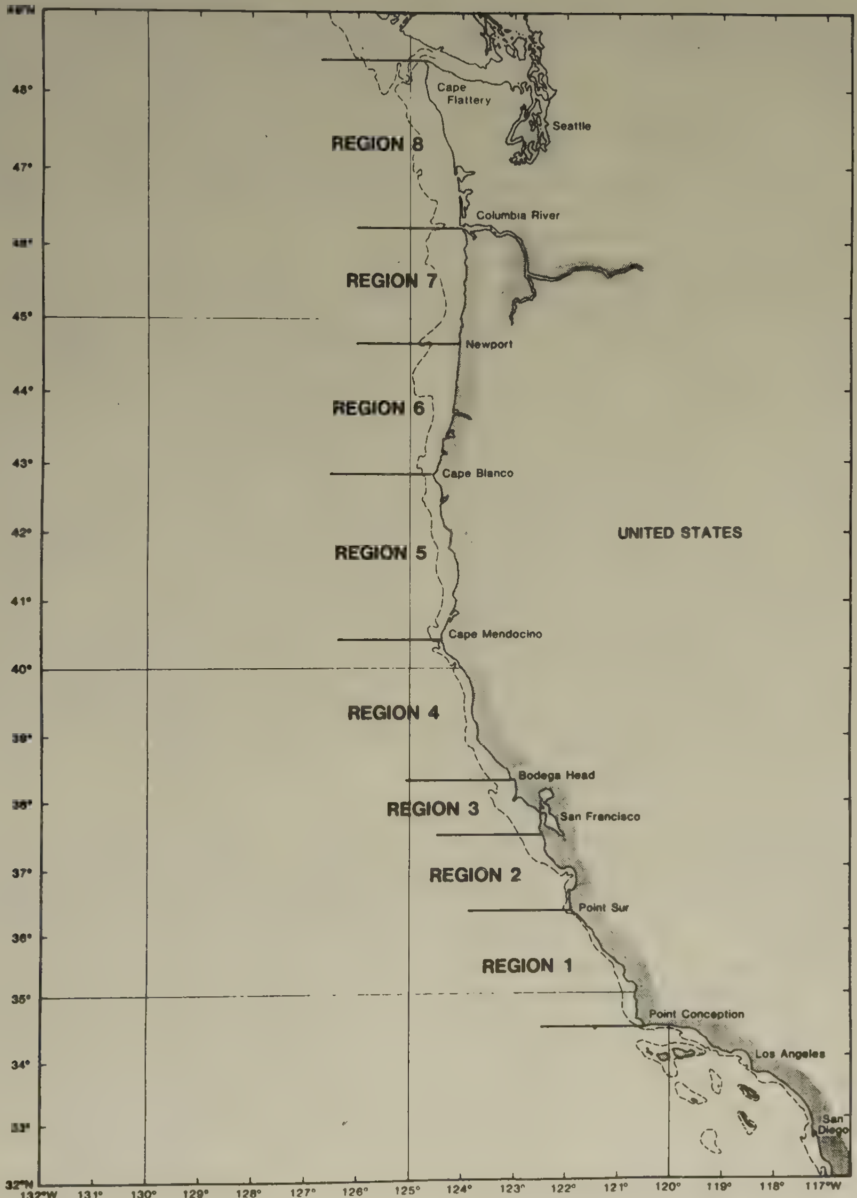
[8] LaBarr, M. S., and D. G. Ainley. 1985. Depth distribution of harbor porpoise off central California: A report of cruises in April and May–June 1985. Report to U.S. National Marine Fisheries Service, Northwest and Alaska Fishery Center, 7600 Sand Point Way N.E., Seattle, WA. Contract No. 41-USC252.

[9] Szczepaniak, I. D. 1987. Abundance and distribution of harbor porpoise (*Phocoena phocoena*) in the Gulf of the Farallones National Marine Sanctuary. Contract report prepared for National Park Service, Point Reyes National Seashore, Point Reyes, CA 94956.

[10] G. Van Blaricom, U.S. Fish and Wildlife Service, University of California, Santa Cruz, CA 93106, pers. commun. August 1986.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Seattle
REGION 8
Columbia River
REGION 7
Newport
REGION 6
Cape Blanco
REGION 5
UNITED STATES
Cape Mendocino
REGION 4
Bodega Head
REGION 3
San Francisco
REGION 2
Point Sur
REGION 1
Point Conception
Los Angeles
San Diego

FIGURE 2.—Geographic regions used as strata in abundance estimation. Broken line indicates the 200 m isobath and delineates likely harbor porpoise habitat.

alone (group size of 1) and larger groups (group size of 3 and greater) ($P = 0.56$).

## Environmental Conditions Affecting Sightings

Sighting efficiency was not significantly affected by rain, fog, or sun glare. Rain/fog conditions were considered "poor" if rain or fog were present within 5 km of the vessel and "good" if neither were present. The distributions of perpendicular sighting distances were not significantly different between these two strata ($P = 0.32$, 0.44, 0.78, and 0.64, respectively, for surveys 1, 2, 3, and 4), and the number of porpoise per kilometer surveyed was higher in the "poor" category for two of the surveys. Sun glare from the water's surface was considered to contribute to "poor" sighting conditions if the sun was within 45° of the trackline in front of the ship. Conditions were considered "good" when the sun was in other positions or was obscured by clouds. As with rain/fog conditions, the distributions of perpendicular sighting distances were not significantly different between these "good" and "poor" sun glare categories ($P = 0.87$, 0.47, 0.30, and 0.55, respectively, for surveys 1, 2, 3, and 4). The number of harbor porpoise per kilometer surveyed were slightly higher in the poor category for three of the surveys. In paired comparisons when glare was present on only one side of the bow, approximately equal numbers of sightings were made on the sides with and without glare (60 vs. 59, respectively). All categories of rain, fog, and glare are included in subsequent analyses.

Sea state did have a significant effect on porpoise sightings. Sea state was categorized as calm (without white-caps, Beaufort sea states 0, 1, and 2) or rough (with white-caps, Beaufort sea states 3, 4, and 5) following the classification used by Holt and Cologne (1987). Distributions of perpendicular distances were not significantly different between these categories for any of the surveys ($P > 0.05$); however for all surveys combined, the number of harbor porpoise detected per kilometer was much lower during rough seas (0.32 $\mathrm{km}^{-1}$) than during calm seas (1.22 $\mathrm{km}^{-1}$). There were insufficient sightings to estimate density for rough seas separately; therefore, rough sea data were excluded in subsequent analyses. For all three surveys, the numbers of harbor porpoise detected per kilometer was higher at Beaufort 0 & 1 than at Beaufort 2, and for survey 3, the distributions of perpendicular sighting distance were significantly different between these categories ($P = 0.03$). Porpoise density is, therefore, estimated separately for Beaufort 0 & 1 and for Beaufort 2 conditions. (For comparison, harbor porpoise abundance was also estimated pooling Beaufort sea states 0, 1, and 2. Estimated abundance was approximately the same by both methods, but the variance was slightly lower using the stratified sea state categories. For this reason, only the stratified estimates are presented here.)

## Helicopter Observations

Helicopter observation of the behavior of harbor porpoise in response to the survey ship were made on only 6 groups of animals. Plots of vessel tracks and movements of the groups are given in the cruise report (see footnote 5). Only in one case was a distinct behavioral change noted in response to the ship. In that case, when the vessel was within 800 m, the group moved rapidly, perpendicular to the path of the vessel and then parallel to and in the opposite direction of the vessel. Observers on the ship saw this harbor porpoise group as they moved rapidly out of the path of the vessel. Observers on the ship also saw 2 of the other 5 groups. Although this sample of behavior is small, movement in response to the survey vessel appeared limited to within 1 km of the vessel and, when it occurred, animals did not travel far from their original positions.

## Porpoise Density

The probability density distributions of perpendicular sighting distances are shown in Figure 3 for surveys 1 and 3 and for Beaufort sea states 0 & 1 and 2. The hazard rate model gave acceptable fits for all sighting distributions ($P > 0.1$) when the truncation criteria was set at 400 m (Table 1). For survey 1, the optimum truncation points were chosen as 400 m for Beaufort 0 & 1 and 800 m for Beaufort 2; for survey 3, this distance was 400 m for both Beaufort sea state categories. The fits of these models are shown in Figure 3. Estimates of density and standard errors are given in Table 2.

## Depth Distribution Model

The model of harbor porpoise depth distribution was based on the relative densities of harbor porpoise at different water depths. Ship survey data were pooled into five depth ranges: 18–37 m (10–20 fathoms), 37–55 m (20–30 fathoms), 55–73 m (30–40 fathoms), 73–91 m (40–50 fathoms), and 91–110 m (50–60 fathoms). Ship surveys are generally not practical inshore of the 18 m isobath, but estimates

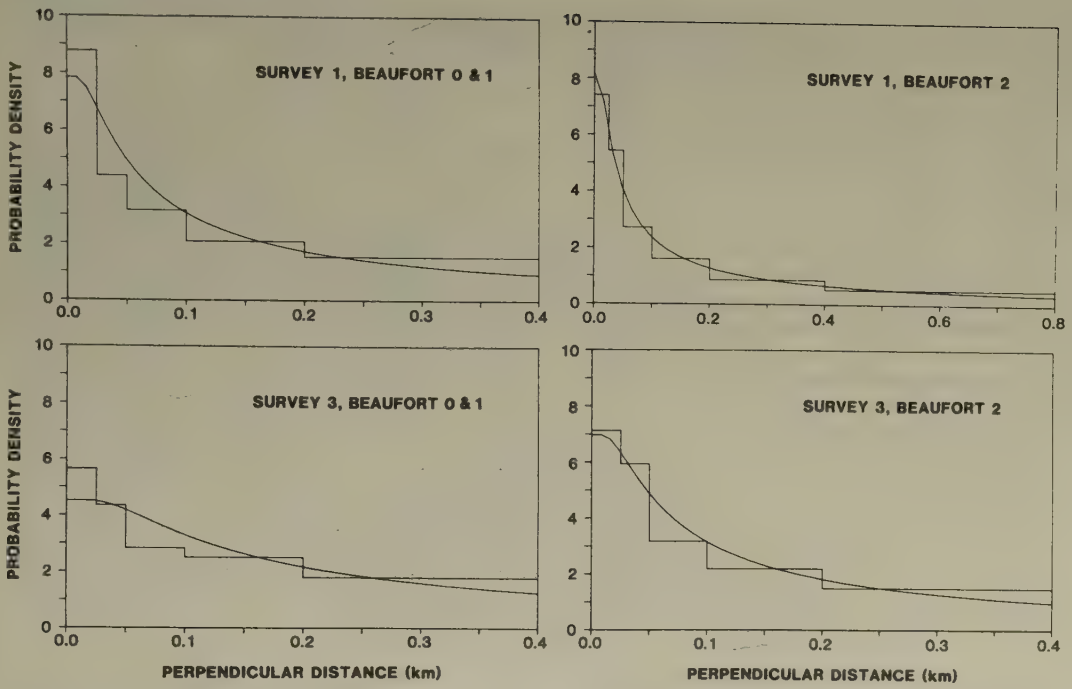

FIGURE 3.—Probability density distributions for perpendicular sighting distances. Histograms indicate observed distributions, and solid lines indicate the best fit of the hazard rate model to these data.

TABLE 1.—Estimated values of the probability density functions evaluated at zero perpendicular distance, $f(0)$. Estimates are based on the hazard rate model and were made for truncation distances of 400, 800, 1,600, and 3,200 m. Estimates are given only if the model gave an acceptable fit to the data ($P > 0.1$). Asterisks indicate $f(0)$ values with the lowest coefficient of variation (parentheses).

| Survey | Beaufort sea state | Truncation distance 400 m | 800 m | 1,600 m | 3,200 m |
|---|---|---|---|---|---|
| 1 | 0 & 1 | 7.85 *<br>(0.23) | 5.31<br>(0.29) | 4.31<br>(0.24) | —<br>— |
| 1 | 2 | 10.48<br>(0.59) | 8.15 *<br>(0.21) | 7.09<br>(0.33) | 5.78<br>(0.51) |
| 3 | 0 & 1 | 4.51 *<br>(0.22) | 3.10<br>(0.66) | 2.69<br>(0.31) | —<br>— |
| 3 | 2 | 6.97 *<br>(0.19) | —<br>— | —<br>— | —<br>— |

from aerial surveys (Barlow et al. 1988) show roughly equal density at 0.61 and 1.85 km from the shore (the latter corresponding approximately to the 18 m isobath). Relative density from ship surveys was measured in the number of sightings per kilometer of searching effort. Relative densities at

TABLE 2.—Density estimates, $D$, for harbor porpoise (km$^{-2}$) along the 18 m isobath in each of eight geographic strata. Density was calculated per Equation (2), using estimates of $f(0)$ (Table 1) which had the lowest coefficients of variation. Values are not adjusted for missed animals. Standard errors are in parentheses.

| Geographic region | Survey 1 Beaufort 0 & 1 | Survey 1 Beaufort 2 | Survey 3 Beaufort 0 & 1 | Survey 3 Beaufort 2 | Pooled estimates |
|---|---|---|---|---|---|
| 1 | 0.0<br>(0.0) | 0.0<br>(0.0) | 0.0<br>(0.0) | 0.1<br>(0.1) | 0.04<br>(0.02) |
| 2 | 1.1<br>(1.0) | 0.0<br>(0.0) | 0.6<br>(0.5) | 0.1<br>(0.1) | 0.51<br>(0.30) |
| 3 | — | 0.0<br>(0.0) | 0.1<br>(0.1) | 0.0<br>(0.0) | 0.03<br>(0.03) |
| 4 | — | 2.5<br>(1.0) | 0.0<br>(0.1) | 6.7<br>(7.2) | 2.83<br>(1.69) |
| 5 | — | 2.1<br>(1.3) | 0.8<br>(0.6) | 0.6<br>(0.3) | 0.91<br>(0.32) |
| 6 | 1.4<br>(0.8) | 2.0<br>(0.6) | 2.5<br>(0.8) | 2.6<br>(0.9) | 2.22<br>(0.40) |
| 7 | 7.9<br>(3.4) | 0.8<br>(0.6) | 2.5<br>(0.6) | 1.3<br>(0.7) | 2.64<br>(0.78) |
| 8 | 1.8<br>(0.8) | 0.0<br>(0.0) | — | — | 1.09<br>(0.45) |
| Total | 2.5<br>(1.1) | 1.3<br>(0.6) | 0.8<br>(0.4) | 1.2<br>(0.5) | 1.33<br>(0.30) |

18–37 m show no consistent relationship to those at 37–55 m or 55–73 m (Table 3), but on average these appear to be approximately equal. Relative densities at 18–37 m are, however, consistently higher than densities at 73–110 m in all areas (Table 3). A total of 236 km were searched in waters deeper than 110 m and no harbor porpoise were seen.

Despite high variability in patterns of depth distribution and lack of ship coverage in shallow waters, some generalizations can be made about the depth distribution of harbor porpoise along the west coast. The relative abundance of harbor porpoise appears to be roughly constant from shore to 55 m, to be markedly lower at 73–110 m, and to be very low in waters deeper than 110 m.

Based on the above relationships, I propose the following preliminary model for the depth distribution of harbor porpoise along the coasts of California, Oregon, and Washington: constant abundance from the coast to the 80 m isobath, linearly decreasing abundance from the 80–120 m isobaths, and zero abundance in waters deeper than 120 m (Fig. 4a). Because considerable uncertainty exists in this model, I propose two alternative models (Fig. 4b, c). Alternative models b and c are less likely than the primary model given because both conflict with some of the available data. The alternative models do, however, encompass the likely range of relative density values and provide a means to evaluate the sensitivity of the abundance estimate to different models of depth distribution.

## Fraction of Missed Animals

The experiment on survey 4 indicates that some trackline groups were seen by 1 group of observers and were missed by the other. A total of 103 sightings was made by both teams, 33 of which were estimated to be within 100 m perpendicular distance from the transect line. Of the 103 total sightings, 85 were detected only by the 5 principal observers, 6 were detected only by the 3 monitor observers, and 12 were detected by both teams. Of the 33 trackline sightings, 20 were detected only by the principal observers, 3 were detected only by the monitor observers, and 10 were detected by both teams. The Petersen estimate of the fraction of trackline porpoise seen by the primary team of 5 observers is thus 0.780 (SE = 0.117, 95% C.L. = 0.45–0.95). This indicates that approximately 22% of trackline sightings are missed by the principal teams of 5 observers.

## Porpoise Abundance

Estimates of porpoise abundance in each of the eight geographic strata are given in Table 4 for the primary model of offshore distribution. Independent estimates are given for survey 1 and for survey 3

TABLE 3.—Relative harbor porpoise abundance observed within the specified depth ranges at a variety of study sites. Relative abundance is measured as number of porpoise sightings made per kilometer. Numbers in parentheses indicate kilometers surveyed.

| | Depth range | | | | |
|---|---|---|---|---|---|
| Location | 18–37 m | 37–55 m | 55–73 m | 73–91 m | 91–110 m |
| Central California[1] | 0.02<br>(89) | 0.08<br>(172) | 0.03<br>(403) | 0.03<br>(279) | 0.01<br>(166) |
| Gulf of the Farallones, CA[2] | 0.29<br>(181) | 0.00<br>(159) | 0.30<br>(133) | 0.00<br>(7) | 0.00<br>(7) |
| Fort Bragg, CA | 0.05<br>(41) | — | 0.05<br>(43) | — | 0.03<br>(35) |
| Coquille Pt, OR | 0.24<br>(43) | — | 0.35<br>(52) | — | 0.08<br>(50) |
| Tillamook Head, OR | 0.50<br>(57) | — | 0.12<br>(52) | — | 0.00<br>(17) |
| Monterey Bay, CA | 0.46<br>(220) | 0.29<br>(76) | — | — | — |
| Russian River, CA | 0.00<br>(26) | 0.30<br>(33) | — | — | — |

[1] Data taken from LaBarr and Ainley (see text footnote 8) assuming an average survey speed of 9 knots.

[2] Data taken from Szczepaniak (see text footnote 9) assuming an average survey speed of 9 knots.

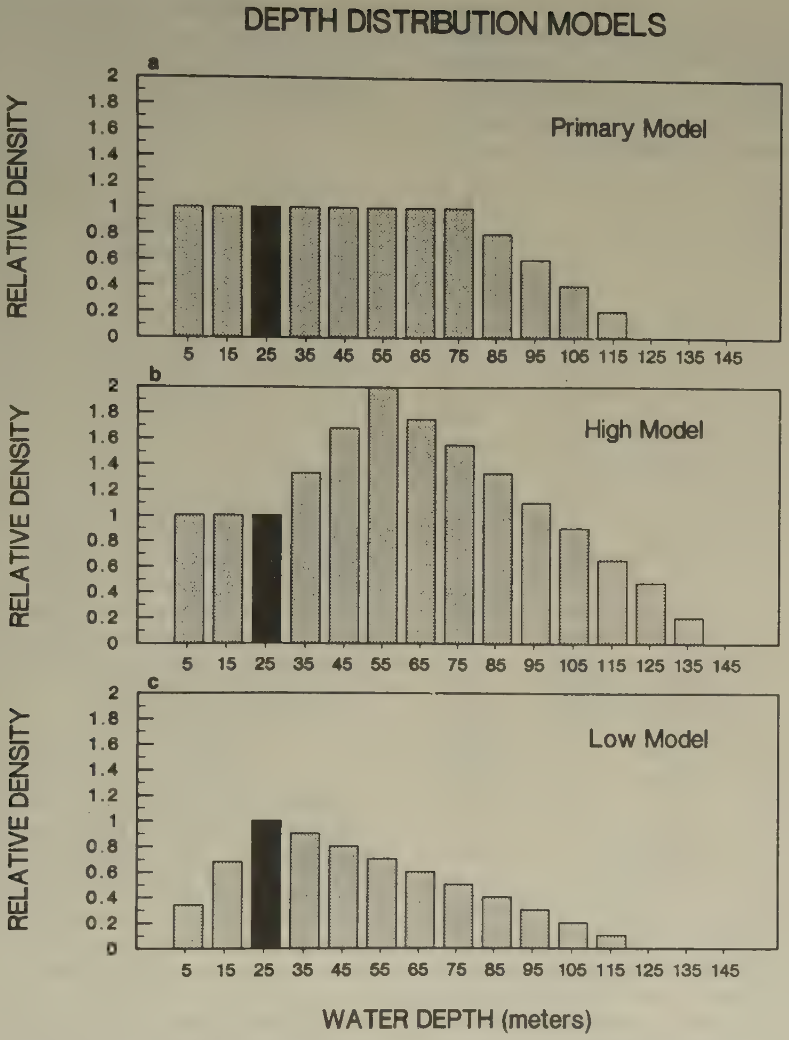

FIGURE 4.—Proposed models for the depth distribution of harbor porpoise expressed as relative densities, $I_k$, within 10 m depth intervals. Density at 20–30 m is assumed to be known and is given a relative value of 1. Figures represent a) a primary model of offshore distribution, b) a high estimate of offshore range, and c) a low estimate.

in each area. Both surveys show similar patterns, with higher abundances in the northern strata (4–8) and very low abundance in strata 1 and 3. Despite similar patterns, differences between the paired estimates are in some cases, large and statistically significant (*t*-tests, $P < 0.05$). Because region 8 was not covered on the third survey, it is not possible to compare estimates of total abundance for the entire coast between surveys. The total abundances for regions 1–7 (Point Conception to the Columbia River) are 46,550 (SE = 10,932) animals and 32,029 (SE = 10,906) animals for surveys 1 and 3, respectively. The difference between these estimates is not statistically significant (*t*-test, $P > 0.05$). Pooling the results of the two surveys, the estimate of harbor porpoise abundance between Point Conception and Cape Flattery in September of 1984 and 1985 is 45,713 (SE = 7,865) animals (Table 4). The same estimate using the alternate models of offshore distribution ranges from 28,769 to 78,019 (Table 5).

TABLE 4.—Estimated abundance of harbor porpoise in each of the eight geographic strata based on the primary model of offshore distribution. Estimates for Beaufort 0 & 1 and for Beaufort 2 were computed separately and then averaged, weighting by transect length. Pooled estimates for the eight strata were obtained as an average of the two surveys, weighting by transect length. All estimates are adjusted for missed animals. Standard errors are in parentheses.

| Geographic region | Survey 1 | Survey 3 | Pooled estimates |
|---|---|---|---|
| 1 | 0 | 126<br>(68) | 96<br>(52) |
| 2 | 2,401<br>(2,180) | 932<br>(646) | 1,459<br>(885) |
| 3 | 0 | 153<br>(158) | 112<br>(116) |
| 4 | 6,909<br>(2,959) | 9,096<br>(9,855) | 7,909<br>(4,784) |
| 5 | 11,245<br>(6,943) | 3,296<br>(1,410) | 4,806<br>(1,745) |
| 6 | 9,061<br>(2,724) | 12,786<br>(3,676) | 11,107<br>(2,363) |
| 7 | 16,934<br>(7,097) | 5,641<br>(2,424) | 10,416<br>(3,311) |
| 8 | 9,808<br>(4,311) | — | 9,808<br>(4,311) |
| Totals | | | |
| Regions 1–3 | 2,401<br>(2,180) | 1,210<br>(669) | 1,667<br>(895) |
| Regions 1–7 | 46,550<br>(10,932) | 32,029<br>(10,906) | 35,904<br>(6,578) |
| Regions 1–8 | 56,358<br>(11,751) | — | 45,713<br>(7,865) |

TABLE 5.—Estimated abundance of harbor porpoise in central California (regions 1–3) and along the entire coast (regions 1–8) based on two alternate models of offshore distribution. All estimates are adjusted for missed animals. Standard errors are in parentheses.

| | Survey 1 | Survey 3 | Pooled estimates |
|---|---|---|---|
| Alternate Model b | | | |
| Regions 1–3 | 3,966<br>(3,602) | 1,986<br>(1,104) | 2,744<br>(1,478) |
| Regions 1–8 | 95,132<br>(19,515) | — | 78,019<br>(13,356) |
| Alternate Model c | | | |
| Regions 1–3 | 1,505<br>(1,367) | 770<br>(421) | 1,054<br>(561) |
| Regions 1–8 | 35,736<br>(7,550) | — | 28,769<br>(4,995) |

# DISCUSSION

## Distribution

Harbor porpoise are not uniformly distributed between Cape Flattery and Point Conception. Although there are no obvious discontinuities within this range, density varies geographically and temporally. The most dramatic temporal changes are between the two September surveys and the January–February survey (Fig. 1). The coasts of Washington and northern Oregon were found to have relatively high densities of harbor porpoise in September, but, despite excellent sighting conditions, very few porpoise were seen there in January. High densities of harbor porpoise were also seen in Monterey Bay on both September cruises and on survey 4 in May. This area was intensively surveyed in February, and few harbor porpoise were seen. As can be seen in Figure 1, adjacent areas tended to have similar densities within a survey. Less consistency is found when the same areas are compared between different surveys.

The apparent changes in distribution could be caused by small changes in depth distributions. The majority of survey effort was along the 18 m isobath. A large fraction of animals could be missed if their depth distribution changed by 10 m or less. More information on depth distributions is needed before the apparent temporal changes in geographic distribution can be interpreted.

## Porpoise Density

Estimates of harbor porpoise density ranged from 0.03 to 2.8 animals/km$^2$ along transect lines in the eight geographic regions (pooled estimates, Table 2). In another study, Szczepaniak (fn. 9) estimated 0–1.9 porpoise/km$^2$ in four study areas in the Gulf of the Farallones, CA. Taylor and Dawson (1984) found 1.2–5.9 porpoise/km$^2$ at study sites in Glacier Bay, AK. Flaherty and Stark[11] estimated 0.8–1.6 porpoise/km$^2$ in Washington Sound. Densities in the present study are therefore within the range of densities found in other areas along the same coast.

Harbor porpoise density was estimated for California, Oregon, and Washington based on aerial surveys that were concurrent with the present study (Barlow et al. 1988). The overall estimate of harbor porpoise density from that study (corrected for missed animals) was 1.79 porpoise/km$^2$. The overall estimate from the ship survey (1.33 porpoise/km$^2$) can be corrected for missed animals to yield an estimate of 1.73 porpoise/km$^2$. Given that the coefficient of variation in the pooled ship estimates is nearly 25%, these estimates are in very close agreement. However, because the aerial estimates are based only on the small fraction of the coastline that was surveyed under optimal conditions, the ship estimates are probably a better representation of porpoise density for the entire coast.

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[11] Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound". Final Report #80-ABA-3584 submitted to National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, NE, Seattle, WA 98115. 84 p.

Of the areas surveyed, harbor porpoise density is highest in northern California and Oregon. The highest density was seen in northern Oregon (region 7) during survey 1. The second highest density was observed in northern California between Bodega Head and Cape Mendocino (region 4) on survey 3.

Two areas in central California (regions 1 and 3) were found to have very low densities. Region 1 includes the Big Sur coastline from Point Conception to Point Sur. This area is characterized by steep depth gradients and hence has little habitat that is suitable for harbor porpoise. Region 1 was relatively well covered, with 378 km of trackline surveyed at Beaufort sea states 0–2. In contrast, region 3 includes the Gulf of the Farallons with its broad coastal shelf within the 100 m isobath. Based on surveys of 764 km, Szczepaniak (fn. 9) estimated 1,033 harbor porpoise are found in the Gulf of the Farallones alone. This is much greater than my estimate of 112 animals in region 3 based on only 175 km of survey effort. Because of his greater amount of search effort in this area, I believe that Szczepaniak's estimates for region 3 are more accurate than mine. Although regions 1 and 3 were both identified as low density areas, more confidence can be placed on this conclusion for region 1 than for region 3.

## Abundance

The size and behavioral characteristics of harbor porpoise make estimating their abundance difficult. Harbor porpoise are small, occur in groups of only a few individuals, and surface without conspicuous splashes; their distribution is extremely patchy. Even with 5 observers, the effective path width that can be searched from a ship is <1 km, and that path width decreases very rapidly in rougher sea states. All of these factors contribute to high variability in the abundance estimates presented here. Seasonal and year-to-year changes in the distribution of harbor porpoise may also contribute to the variability seen within geographic strata. These are, however, the best (and, for some regions, the only) estimates of harbor porpoise abundance for the study area.

Although there are no prior estimates for Oregon or Washington coasts, Dohl et al. (fn. 4) estimated harbor porpoise abundance in central and northern California. Their estimates range from 3,000 harbor porpoise in autumn to 1,600 in summer, which correspond (approximately) to the pooled estimate of 11,457 for regions 1–4 based on the present study. There are, however, several problems with the application of their methods to the estimation of harbor porpoise abundance. In a direct comparison with shore counts, Kraus et al. (1983) showed that observers on aircraft saw only 10–20% of harbor porpoise groups. Dohl et al. (fn. 4) did not apply a correction to account for harbor porpoise groups that are submerged at the time the aircraft passed. Also, Dohl et al. did not stratify estimates by distance from shore or depth. Although most of their harbor porpoise sightings were within 0.5 km (0.25 nmi) of shore, their density estimates were extrapolated to an area extending 166 km from the coast. Estimates from the current study are based on better methodology than previous estimates.

In addition to exposed coastal habitats, harbor porpoise are also found in bays along the coasts of California, Oregon, and Washington. Goetz (1983) reported that harbor porpoise are found throughout the year in Humboldt Bay, CA. Harbor porpoise have been seen in San Francisco Bay, but are described as rarely present[12]. Abundance of harbor porpoise in inland waters may, however, vary seasonally (Taylor and Dawson 1984). No estimates exist for the total number of harbor porpoise inhabiting bays. Survey effort in the present study was limited to exposed coastal areas (including Monterey Bay, but excluding San Francisco Bay, Humboldt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor). If harbor porpoise density in bays were the same as that which was observed along the 18 m isobath, population sizes presented here could be increased by approximately 3.1% to account for porpoise inhabiting 900 km$^{-2}$ (the approximate combined area of Humboldt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor).

## Line Transect Assumptions

Biases in abundance estimates can be an even greater problem than high variability. In the case of estimates presented here, biases could be introduced if the assumptions of line transect sampling are not met (Burnham et al. 1980; Hammond and Laake 1983). Of these assumptions, the most relevant to this study are 1) the area must be sampled randomly or the animals must be randomly distributed within the area; 2) all groups on the trackline must be detected; and 3) group size must be estimated without error. These assumptions will be addressed below.

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[12] Szczepaniak, I. D., and M. A. Webber. 1985. Status of the harbor porpoise (*Phocoena phocoena*) in the eastern North Pacific, with an emphasis on California. Contract report to the Center for Environmental Education, Washington, D.C., 52 p.

To address the first assumption (random distribution), cruise tracks were chosen to systematically cover the coast from Point Conception to Cape Flattery. Because the surveys were designed to cover the entire longshore range of harbor porpoise in this area, randomly placed survey tracks were deemed unnecessary. Although some areas of the coast were missed, these locations were determined by weather and were presumably not correlated with porpoise abundance. Surveys were, however, limited to a very narrow strip along the 18 m isobath. Initially, the choice of this survey track was based on the observation that, in aerial surveys, harbor porpoise were usually found within 0.5 km (0.25 nmi) of the shoreline in California (Dohl et al. fn. 4). The 18 m isobath was simply the shallowest reasonable working depth for the NOAA survey ships. In the course of these surveys, it was found that harbor porpoise are commonly distributed much further from the coast than 0.5 km and that one survey track could not adequately cover their habitat. The offshore distribution of harbor porpoise is not random, but is related to water depth, distance from shore, or both. The model from which I extrapolated density at 18 m to density at other depths was based on a rather limited sample at a few locations along the coast. The assumption of random search in offshore areas was not met. Additional work is required to evaluate the effect of this.

The second assumption is that 100% of the animals in the immediate vicinity of the trackline were detected. Animals near the trackline can be missed because they move away from the path of the ship, because they do not surface within the visual range of the observers, or because the observers fail to detect animals that do surface. Any of these would result in a negative bias and an underestimation of porpoise abundance using line transect methods. These three problems are considered in more detail.

West-coast harbor porpoise are commonly said to avoid vessels (Flaherty and Stark fn. 11; Szczepaniak and Webber fn. 12) and may be missed or not counted in the proper perpendicular distance category for this reason. On the surveys, the majority of harbor porpoise were oriented roughly parallel to the ship at the time they were sighted and were swimming parallel to the ship and in the opposite direction (see footnote 5). This was also observed in one instance from the helicopter; however, in that case the group first moved perpendicular to the path of the ship. These observations indicate that harbor porpoise are reacting to the ship before they are seen by observers. Reaction to and avoidance of the ship does not necessarily mean that estimates of trackline density are biased if animals are detected before they travel an appreciable distance from the trackline. In several instances, harbor porpoise surfaced within 50 m of the ship and directly in its path. These animals appeared startled and quickly moved to avoid the ship. In these cases, the rapid movement of the animals and splashes associated with that movement made the animals more visible to observers. Because avoidance behavior may make harbor porpoise more visible and because the distributions of perpendicular distance show only a single mode (at the origin), vessel avoidance probably does not introduce a large bias in harbor porpoise abundance estimation. More work is needed in this area.

Harbor porpoise near the trackline may also be missed if they either inadvertently or intentionally do not surface within the visual range of the observers. Typical mean dive times for harbor porpoise have been measured as 1.5–2.3 minutes (Glacier Bay, AK; Taylor and Dawson 1984), 1.8 minutes (northern Oregon; B. Taylor[13]), and 0.4–1.4 minutes (Bay of Fundy; Watson and Gaskin 1983). The ships' speed during surveys was approximately 18.5 km/h or 310 m/min; thus, in 2 minutes the ship would travel 620 m. The average distance at which animals were first seen was 704 m from the ship. If individual dive times were appreciably longer than 2 minutes, some trackline individuals would not be detected by observers. In data collected in northern Oregon, 16% of dive times were greater than 2.5 minutes (B. Taylor fn. 13). In addition, harbor porpoise have been reported to increase dive times up to 7 minutes in the presence of boat traffic (Flaherty and Stark fn. 9). (This latter estimate is considerably longer than any other published estimate, and it is possible that those researchers missed one or more surfacings). Helicopter observations in Monterey Bay indicated that porpoise groups did not extend dive times in the presence of the survey vessel (see footnote 5). This area might not be representative, however, because harbor porpoise may be more accustomed to vessel traffic there than along the majority of the coast. It is likely that some harbor porpoise are missed because they do not surface near the vessel; however, it is not possible to quantify this source of bias without additional study.

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[13] B. Taylor, Department of Biology, University of California, San Diego, CA 92093, pers. commun. August 1986.

Trackline animals may be missed even if they do not avoid the ship and do surface within visual range of the observers if their surfacing is not detected. In another study comparing ship surveys to aerial and shore surveys, Kraus et al. (1983) found that observers on ships saw only about 50% of the harbor porpoise in an area. In that study, however, ship observers stood only 2.5 m above the sea surface (versus 10 m in this study), and the estimate of 50% was based on all groups, not just on trackline animals. Based on the experiment using monitor observers in the present study, an estimated 22% of harbor porpoise that surface on the trackline are missed by the usual team of 5 observers. If this is underestimated by some percentage, population size would be underestimated by the same percentage.

The third critical assumption is that group size is estimated without error. In the case of harbor porpoise, group size is small and estimates are typically based on actual counts. For tropical dolphins, which school in groups of several hundreds, the problem of group size estimation is more acute (Holt and Powers 1982; Hammond and Laake 1983). Only in two instances did harbor porpoise group size exceed 20: in Monterey Bay and near Point Arena, both in California. Excluding these two sightings, mean group sizes are 2.05, 2.33, 2.03, and 1.59 for surveys 1, 2, 3, and 4 (respectively); including the two sightings, means are 2.30 and 2.26 for surveys 1 and 3. These values are comparable to other estimates of mean group size for coastal populations of harbor porpoise: 2.2 based on aerial surveys in California (Dohl et al. fn. 4), 2.6 based on ship surveys in the Gulf of the Farallons (Szczepaniak and Webber fn. 12), 2.3 based on shore surveys in northern Oregon (see footnote 5), and 2.75–3.23 based on aerial surveys along California, Oregon, and Washington (Barlow et al. 1988). The consistency of all these estimates from different platforms indicates that group size estimation from ships is not likely to be a major source of bias in abundance estimation.

### Variance Estimation

Although the estimates of standard error for abundance and density are very high, these may still be underestimates because the choice of a truncation criterion was based on minimizing variance and because all possible sources of sampling errors were not considered. The model upon which relative abundance in the various depth strata was based is too crude to allow reasonable estimates of its variability. Estimates based on alternate models of depth distribution indicate that abundance estimation is relatively sensitive to the choice of models. Additional field work may help refine this model and allow estimation of variance for the parameters $I_k$ in Equation (4).

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## LITERATURE CITED

ADAMS, L.
1951. Confidence limits for the Petersen or Lincoln index used in animal population studies. J. Wildl. Manage. 15: 13–19.

BARLOW, J., C. OLIVER, T. D. JACKSON, AND B. L. TAYLOR.
1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. Fish. Bull., U.S. 86:433–444.

BUCKLAND, S. T.
1985. Perpendicular distance models for line transect sampling. Biometrics 41:177–195.

BURNHAM, K. P., AND D. R. ANDERSON.
1976. Mathematical models for nonparametric inferences from line transect data. Biometrics 32:325–336.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE.
1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. No. 72, 202 p.

BUTTERWORTH, D. S.
1982. On the functional form used for g(y) for Minke whale sightings, and bias in its estimation due to measurement inaccuracies. Rep. int. Whal. Comm. 32:883–888.

CHAPMAN, D. G.
1951. Some properties of the hypergeometric distribution with applications to zoological censuses. Univ. Calif. Publ. Stat. 1:131–160.

CRANDALL, W. C.
1915. II. The kelp beds from lower California to Puget Sound. *In* F. W. Cameron (editor), Potash from kelp, 122 p. U.S. Dep. Agric. Rep. No. 100.

EFRON, B.
1982. The jackknife, the bootstrap and other resampling plans. CBMS Regional Conference Series in Applied Mathematics 38, 92 p. Society for Industrial and Applied Mathematics, Phila.

GASKIN, D. E.
1984. The harbour porpoise (*Phocoena phocoena* L.): regional populations, status, and information on direct and indirect catches. Rep. int. Whal. Comm. 34:569–586.

GOETZ, B. J.
1983. Harbor porpoise (*Phocoena phocoena* L.) movements in Humboldt Bay, California and adjacent ocean waters. MS Thesis, Humboldt State University, Humboldt, CA, 118 p.

GOODMAN, L. A.
1960. On the exact variance of products. J. Am. Stat. Assoc. 55:708–713.

HAMMOND, P. S., AND J. L. LAAKE.
1983. Trends in estimates of abundance of dolphins (*Stenella* spp. and *Delphinus delphis*) involved in the purse-seine fishery for tunas in the eastern tropical Pacific Ocean, 1977–81. Rep. int. Whal. Comm. 33:565–588.

HOLT, R. S.
In press. Estimation of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Mar. Mamm. Sci.

HOLT, R. S., AND J. COLOGNE.
1987. Factors affecting line transect estimates of dolphin school density. J. Wildl. Manage. 51:836–843.

HOLT, R. S., AND J. E. POWERS.
1982. Abundance estimation of dolphin stocks involved in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-23, 95 p.

KRAUS, S. D., J. R. GILBERT, AND J. H. PRESCOTT.
1983. A comparison of aerial, shipboard, and land-based survey methodology for the harbor porpoise, *Phocoena phocoena*. Fish. Bull., U.S. 81:910–913.

LAAKE, J. L., K. P. BURNHAM, AND D. R. ANDERSON.
1979. User's manual for program TRANSECT. Utah State University Press, Logan, Utah, 26 p.

POLLOCK, K. H., AND W. L. KENDALL.
1987. Visibility bias in aerial surveys: A review of estimation procedures. J. Wildl. Manage. 51:502–510.

TAYLOR, B. L., AND P. K. DAWSON.
1984. Seasonal changes in density and behavior of harbor porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. Rep. int. Whal. Comm. 34:479–483.

WATSON, A. P., AND D. E. GASKIN.
1983. Observations on the ventilation cycle of the harbour porpoise (*Phocoena phocoena* L.) in the coastal waters of the Bay of Fundy. Can. J. Zool. 61(1):126–132.

YATES, F.
1953. Sampling methods for censuses and surveys. Hafner Publishing Co. Inc., N.Y., 401 p.

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# HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: II. AERIAL SURVEYS

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## ABSTRACT

We conducted aerial surveys in September 1984 and September and October 1985 to determine the abundance of harbor porpoise along the coasts of California, Oregon, and Washington. Two observers and a recorder searched along predetermined transect lines at 0.61 and 1.85 km offshore. Strip transect methods were used. A total of 366 groups of harbor porpoise were seen in the 9,500 linear kilometers that were surveyed. Apparent density was significantly affected by sea state and cloud cover. Using observations made during optimal conditions (clear skies and calm seas), apparent harbor porpoise density averaged 0.56 animals km$^{-2}$. Behavioral observations from shore and from a helicopter indicated that porpoise are near the surface only 23.9% of the time. To account for this, porpoise density was multiplied by a factor of 3.2, resulting in an adjusted estimate of 1.79 animals km$^{-2}$. Only a small percentage of the total area inhabited was surveyed under optimal sighting conditions, hence density estimates were not extrapolated to estimate total porpoise abundance. Harbor porpoise density showed similar patterns to those measured from ship surveys, and adjusted aerial estimates are approximately equal to ship estimates.

Harbor porpoise, *Phocoena phocoena*, are subject to mortality in the halibut set net fishery in central California (NMFS[4]; Diamond and Hanan[5]). To evaluate the significance of this mortality, an estimate of population size is needed. Two aerial surveys and three ship surveys were conducted from 1984 to 1986 to gather information on harbor porpoise abundance along the coasts of California, Oregon, and Washington. Observations were also made from shore-based stations and from a helicopter to provide ancillary information needed for population estimation. Results and population estimates from the ship surveys are reported by Barlow (1988). Preliminary results from the 1984 and 1985 aerial surveys were presented by Oliver and Jackson[6] and Oliver[7], respectively. Here we present population density estimates based on the aerial surveys and on shore and helicopter observations.

The aerial surveys were flown in September of 1984 and in September and October of 1985 from Point Conception, CA to Cape Flattery, WA. Surveys were coordinated by the National Marine Fisheries Service (NMFS) in collaboration with the California Department of Fish and Game, the Oregon Department of Fish and Wildlife, and the Washington Department of Wildlife. Survey design was based on information given by Dohl et al.[8] regarding harbor porpoise distribution in California. They reported that harbor porpoise were usually

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[4] NMFS. 1980. A report based on the workshop on stock assessment and incidental take of marine mammals involved in commercial fishing operations. January 1980. Available from National Marine Fisheries Service, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[5] Diamond, S. L., and D. A. Hanan. 1986. An estimate of harbor porpoise mortality in California set net fisheries: April 1, 1983 through March 31, 1984. Adm. Rep. SWR-86-15, 40 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[6] Oliver, C. W., and T. D. Jackson. 1987. Occurrence and distribution of marine mammals at sea from aerial surveys conducted along the U.S. west coast between December 15, 1980 and December 17, 1985. Adm. Rep. LJ-87-19, 189 p. Available from National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[7] Oliver, C. W. 1986. Trip report: 1985 harbor porpoise aerial survey, September 9 to October 15, 1985. Adm. Rep. LJ-86-21, 29 p. Available from National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[8] Dohl, T. P., R. C. Guess, M. L. Duman, R. C. Helm. 1983. Cetaceans of central and northern California, 1980–83: status, abundance, and distribution. Report prepared for U.S. Minerals Management Service, contract #14-12-0001-29090.

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found within 0.25 nautical miles (nmi) of the shoreline. We therefore designed our aerial surveys to cover a very narrow coastal band. Subsequent information from ship surveys (Barlow 1988) has shown their distribution to extend considerably farther from the coast. Therefore, estimates of porpoise density from aerial surveys apply to a relatively small portion of harbor porpoise habitat. For this reason we do not estimate population size by extrapolating aerial density estimates to the entire area inhabited. The density estimates presented here are used to corroborate estimates based on ship surveys and to estimate density for areas that were too shallow to be surveyed by ship.

Based on previous studies of dive times (Watson and Gaskin 1983; Taylor and Dawson 1984) we expected a proportion of the harbor porpoise to be diving and therefore missed by aerial observers. Shore-based studies were conducted in September 1985 from cliffs in northern Oregon to determine average dive times for west-coast harbor porpoise. Helicopter observations were made in April and May 1986 in Monterey Bay and near Bodega Head, CA to gather dive time information and obtain a direct measure of the fraction of time that harbor porpoise groups are visible from the air. These two samples did not differ significantly from previous samples of harbor porpoise in Alaska, so all samples were pooled to adjust estimates of porpoise density from aerial surveys to account for the probability of missing submerged animals.

## METHODS

### Aerial Survey Methods

Strip transect methodology (Seber 1973) was used during the aerial surveys. This method assumes that all individuals within a transect strip are detected. Transect lines were flown parallel to the coast line at distances of 0.61 and 1.85 km (0.33 and 1.0 nmi) offshore. Transect strips of equal width were surveyed on both sides of the aircraft. The margins of the strips were denoted by tape marks or streamers on the wing struts. Strips were divided into inside and outside swaths of unequal width (Fig. 1) by a third tape mark or streamer between the other two. When porpoise were sighted within the transect strip, the pilot was directed to leave the transect line and circle over the porpoise to obtain an accurate count of the number within the original group that was sighted. If additional groups or individuals were sighted during this circling, they were excluded from density estimates. Porpoise density, $x$, was calculated as the number of individuals sighted within a transect, $n$, divided by the product of the transect width, $w$, times the distance, $d$, that was flown:

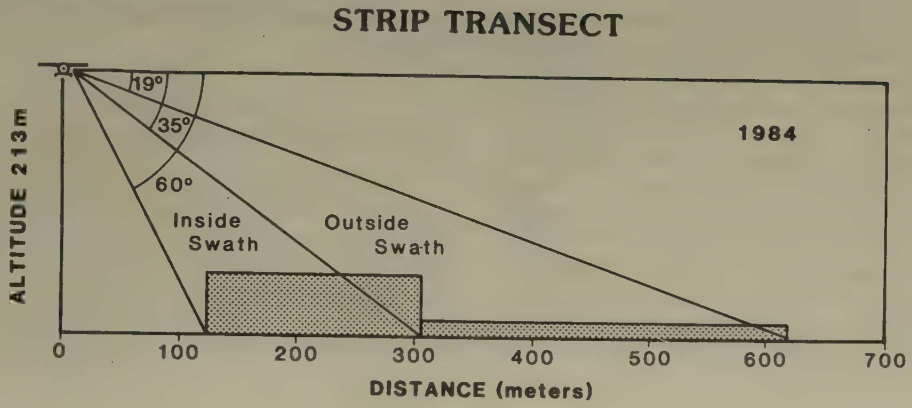
$$x = n/(W \cdot d) \qquad (1)$$

We used both single and twin-propeller, high-wing, 4-passenger aircraft in our surveys. The search team consisted of two observers seated in the right and left passenger seats. A data recorder sat in the copilot's seat and did not search. If the recorder sighted animals that were missed by the observers, these were noted but were not included in density estimates. The planes were flown at an altitude of 213 m (700 feet) and at an airspeed of 158–167 km/h (85–90 knots). The original survey plan called for all sections of the coast to be covered twice on each survey. This was accomplished in 1984, but poor weather in 1985 resulted in the Washington coast and part of the Oregon coast being covered only once. The dates flown and areas covered are given in Table 1.

TABLE 1.—Dates, areas covered, and observer teams during aerial surveys for harbor porpoise. Geographic regions refer to those shown in Figure 2. Observer team refers to a pair of individuals.

| Date | Regions covered | Observer team | Distance to shore (km) |
|---|---|---|---|
| 9/09/84 | 7,8 | A | 0.61 |
| 9/10/84 | 5,7 | A | 0.61 |
| 9/11/84 | 5,6 | A | 0.61 |
| 9/13/84 | 1,2,3,4,5 | B | 0.61 |
| 9/14/84 | 1,2,3,4,5 | B | 0.61 |
| 9/17/84 | 1,2,3,4 | B | 0.61 |
| 9/18/84 | 1,2,3,4 | B | 0.61 |
| 9/11/85 | 6,7 | C | 0.61 |
| 9/16/85 | 1,2,3 | D | 0.61 |
| 9/17/85 | 4 | D | 0.61 |
| 9/18/85 | 4,5 | D | 0.61,1.85 |
| 9/19/85 | 4,5 | D | 0.61,1.85 |
| 9/20/85 | 2,3 | D | 1.85 |
| 10/04/85 | 7,8 | E | 0.61 |
| 10/14/85 | 1,2,3 | D | 1.85 |
| 10/15/85 | 4,5 | D | 1.85 |

Data gathered on both the 1984 and 1985 surveys were similar in format. Recorded data on sighting conditions included Beaufort sea state, a measure of cloud cover, a code indicating the presence of haze or fog, sun position relative to the aircraft, and a subjective measure of the observers' ability to see into the water through turbidity, surface reflection and diffraction. The latter was called surface penetration and was recorded separately for each of the



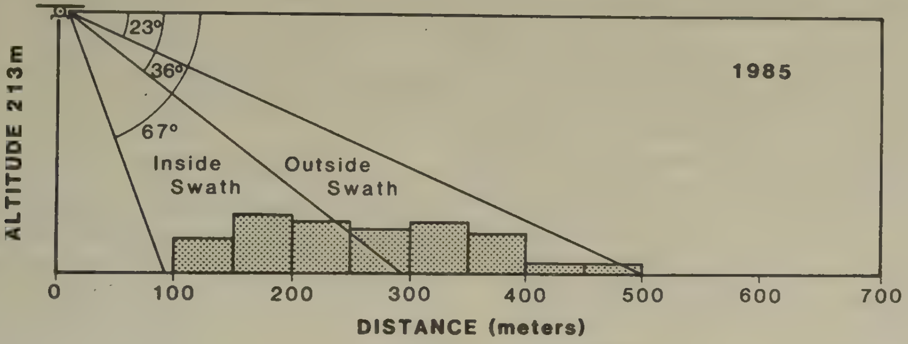


FIGURE 1.—Configuration of transect strip widths and distributions of perpendicular sighting distances for aerial surveys in 1984 and 1985. Angles are given as declinations from horizontal. Histograms indicate the relative number of porpoise seen in the given distance interval.

four swaths (inside and outside on both sides of the aircraft). In severe sun glare conditions, searching was discontinued for one or both swaths on one side of the aircraft. Additional data included individual observer numbers, date, time, and position (measured to 10ths of minutes of latitude and longitude). All of these data were recorded at the beginning and end of continuous transects and whenever conditions changed or a sighting was made. Additional data were recorded for marine mammal sightings, including a code for the species of animal seen, an estimate of the number of individuals, a code indicating on which side of the aircraft the animals were seen, and a code indicating in which of the swaths the animals were found (inside, outside, or, if the animals were not within the designated strips, neither).

An attempt was made to gather the above information in a similar manner for both surveys. Some differences in subjective measures of sighting conditions could, however, be expected because there was no overlap in observers between years. In addition, there were some differences in design between the 1984 and 1985 surveys. In 1984, the inside and outside swaths were from 123 to 305 m and from 305 to 620 m, respectively (as measured from the midline of the transect). The margins of these swaths corresponded to declinations angles of 19°, 35°, and 60° (Fig. 1). In 1985, the swaths were 91–294 m and 294–503 m and corresponded to declination angles of 23°, 36°, and 67° (Fig. 1). In 1984, effort was concentrated on the inside swath and the outside swath was not intended for abundance estimation. The change in swath size was intended to reduce the total area being searched, thus potentially allowing the outer swath to be used for density estimation. In 1985, effort was divided equally between the two swaths. During the 1985 surveys the declination angle to marine mammals was measured when the animals were perpendicular to the aircraft using hand-held inclinometers. Declination angles were not measured during the 1984 survey.

Distance to the coast was monitored using declination angles (19° for 0.61 km and 6° for 1.85 km). On the 1984 survey, this distance was 0.61 km for the entire survey. During the 1985 survey, we surveyed at both 0.61 and 1.85 km from the coast. In 1984, the coast was taken to be the outer limit of the surf zone. In 1985, the coast was taken to be the outer limit of the surf zone or, if kelp beds were present, the outer margin of those beds.

## Shore Observation Methods

Observations of harbor porpoise diving behavior were made from rocky headlands in northern Oregon (Tillamook Head, Neahkahnie Mountain, Cape Meares, and Cape Lookout) immediately before the second aerial survey (7–11 September 1985). Observers were equipped with 7×50 binoculars with compasses and ocular reticles and a single 20×120 binocular. Ventilation data were collected whenever possible and included the number of animals at the surface and the length of time spent at the surface. Observations were recited aloud by the observer and were written down by a second person or were recorded onto magnetic tape. The ventilation cycle typically consisted of a period with several surfacing rolls and breaths (which we call a surfacing series) followed by a much longer period of submergence (which we call a dive). This dive cycle corresponds to ventilation pattern B as described by Watson and Gaskin (1983) for harbor porpoise in the Bay of Fundy and the pattern described by Taylor and Dawson (1984) for porpoise in Glacier Bay.

## Helicopter Observation Methods

Behavioral observations were also made by three observers in a 4-passenger, jet-turbine helicopter. Upon locating a group of harbor porpoise, a fluorescein dye marker was dropped and the helicopter hovered or circled slowly above the group at an altitude of approximately 300 m. The number of animals, the time they were visible at the surface, and the dive times were recorded, along with information on cloud cover, sea state, and water turbidity. Each behavioral session was given a subjective rating based on how well the observers could follow the group and obtain accurate dive times. Only sessions with good or excellent ratings were included in analyses.

## Probability of Missing Submerged Animals

Given that a porpoise would be within the visual range of an observer, the probability that it will be at the surface during the passage of the aircraft is related to the average time it spends at the surface, $s$, the average time spent below the surface, $d$, and the window of time during which it is within the visual range of an observer, $t$. This probability was calculated as

$$Pr(\text{being visible}) = \frac{s + t}{s + d}. \qquad (2)$$

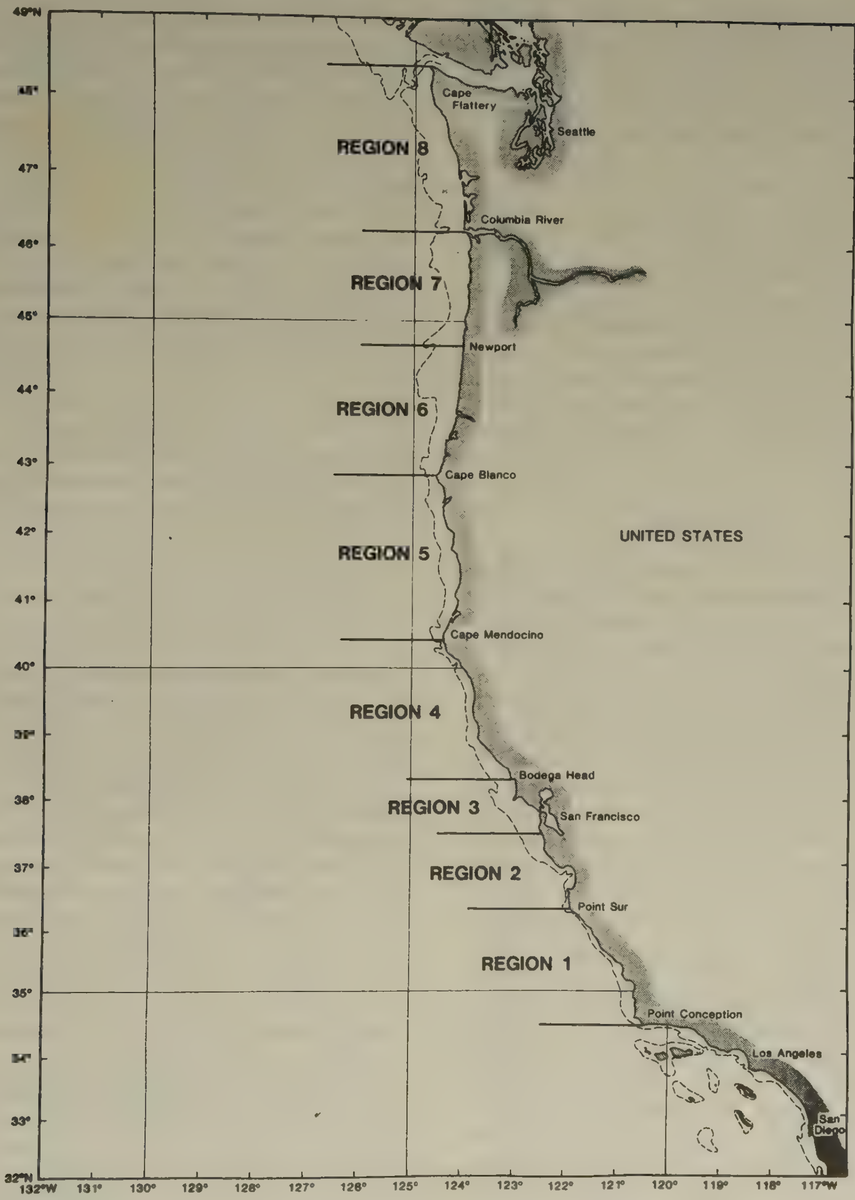
The probability of missing a submerged animal is equal to the complement of this value.

## Density Estimation

Density of harbor porpoise was estimated as the number of animals seen divided by the area searched (Equation (1)). This raw density estimate was adjusted by dividing by the probability that an animal would be visible from the air at any given instant (Equation (2)). The area searched was estimated as the swath widths times the lengths of the transects. Transect lengths were calculated as the sum of the great circle distances between successive position fixes. Densities were calculated for each of the eight statistical regions used by Barlow (1988) (Fig. 2).

The statistical difference in harbor porpoise density between different sighting conditions or different areas was tested using the raw density estimates. Density estimates for short transects were frequently zero, thus violating the parametric assumptions of normally distributed, homoscedastic error. Nonparametric tests were therefore chosen for density comparisons. In discussing statistical tests, a transect segment refers to the length of transect line between two successive position fixes and are typically <20 km. The measured variables relating to sighting conditions are constant within a segment, and because each sighting is accompanied by a new position fix, a segment will contain at most, one sighting.

Whenever applicable, the Wilcoxon paired-sample test (Wilcoxon 1945) was used to test one factor while controlling for as many other factors as possible. Ten paired measures of density were created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Seattle
REGION 8
Columbia River
REGION 7
Newport
REGION 6
Cape Blanco
REGION 5
UNITED STATES
Cape Mendocino
REGION 4
Bodega Head
REGION 3
San Francisco
REGION 2
Point Sur
REGION 1
Point Conception
Los Angeles
San Diego

FIGURE 2.—Geographic regions used as strata in density estimation.

by adding all appropriate transect segments to a linear array and dividing that array into 10 equal parts.

When paired tests were not applicable, nonparametric ANOVA models were used. For simple comparisons, the Kruskal-Wallis single-factor analysis of variance was used (Kruskal and Wallis 1952). For two-way comparisons, we used a two-factor extension of the Kruskal-Wallis test (Scheirer et al. 1976). For both tests, three replicate measures of density were created for each cell by randomly assigning transect segments as replicate 1, 2, or 3.

A principal assumption of strip transect methods is that all individuals within the designated strip are counted. Assuming that the fraction of diving animals does not vary with sighting conditions, any effect of sighting conditions on apparent density is likely due to missed animals. In any instance where we show that poorer sighting conditions result in a significant decrease in apparent density (one-tailed for paired tests, two-tailed for ANOVA tests), we eliminate the category of sighting conditions which resulted in that lower estimate. If it is not possible to predict which category would be worse a priori in paired tests (e.g., right swath vs. left), two-tailed probabilities are used. Although we cannot be sure of eliminating all biases using these methods, this pattern of data paring should avoid much of the bias due to missed animals.

## RESULTS

In 1984, 247 groups of harbor porpoise (680 individuals) were seen within transect strips which covered a linear distance of 5,763 km. In 1985, we saw 119 groups (384 individuals) in surveys of 3,715 km. Mean group sizes were 2.75 and 3.23 individuals, respectively, for 1984 and 1985. For 1984, the relative frequencies of individuals seen within the inside and outside swaths are illustrated in Figure 1. For 1985, the perpendicular distances from the trackline to the animals were calculated from declination angles, and the relative distribution of sightings is shown in Figure 1 as a function of perpendicular distance.

### Inside vs. Outside Swath

For 1984 data, only the inside swaths were used, but for 1985 both inside and outside swaths were considered for density estimation. For 1985, we tested whether the density in the inside swaths was greater than the density of the outside swaths. We only considered cases when the water surface penetration codes were equal in both the inside and outside swaths. Data for inside and outside were thus paired, with all other sighting factors equal. For 1985, the density in the inside was greater (0.09 vs. 0.06 porpoise/km$^2$), but this difference was not significant ($P > 0.10$).

### Surface Penetration

Observers used a subjective coding system to describe their ability to see through the sea surface. Cloud cover, haze, and water turbidity contributed to poor surface penetration. In 1984, observers used codes to indicate good and poor conditions; in 1985, observers used codes for excellent, good, and poor. There were frequent cases when observers recorded different codes for the inside swaths on opposite sides of the plane; hence, paired tests were again appropriate. For 1984, we tested whether density in the "good" category was higher than density in the "poor" category. When surface penetration was different in the inside swaths on opposite sides of the plane, mean density in the "good" category was higher than in the "poor" category (0.16 vs. 0.12 porpoise/km$^2$), but this difference was not significant ($P > 0.25$). For 1985, no tests were necessary because the mean density in "excellent" category was lower than in the "good" category, and likewise, density in the "good" was lower than in the "poor" category. All categories of water surface penetration were included in subsequent analyses.

### Effects Due to Observers and Side of the Plane

Sightings were classified based on which observer made the sighting and on whether the sighting was on the inshore or offshore side of the aircraft. In fact, these two classifications were confounded in 1985 because the two principal observers were situated on the same sides of the aircraft for most of this survey. Effects of these classifications on density estimation were considered together. Survey teams were defined as pairs of observers who worked together. There were two such teams for 1984 and three for 1985 (Table 1). Only one of the teams in 1985 had sufficient numbers of sightings to be considered here. Statistical tests were based on paired cases during which both members of the sighting team were searching.

For 1984, porpoise density on the offshore side of the airplanes was greater than on the inshore side for both team A and team B (Table 2). The difference in density estimates between observers was less than the difference between inshore and off-

TABLE 2.—Relative harbor porpoise densities (km$^{-2}$) for teams of observers. Density estimates are stratified by inshore and offshore sides of the aircraft and by individual observers.

| Observer team | Inshore | Offshore | Observer 1 | Observer 2 |
|---|---|---|---|---|
| A | 0.275 | 0.425 | 0.320 | 0.380 |
| B | 0.168 | 0.244 | 0.232 | 0.179 |
| D | 0.281 | 0.164 | 0.300 | 0.146 |

shore (Table 2), and neither was statistically significant. For 1985, the opposite was seen; the density on the inshore side was greater than on the offshore side and this difference was less than the difference between observers (Table 2), but again, neither difference was statistically significant. In 1984, both observers had previous experience doing aerial surveys, but in 1985, the observer with the lower density estimates had no previous experience in cetacean surveys. Experience may be a factor in density estimates from strip transects, but since the inexperienced observer was always on the same side of the plane, it was not possible to test this with a factorial design.

### Area and Sea State

Analysis of research vessel data (Barlow 1988) indicated two geographic regions in California with low porpoise density (regions 1 and 3 in Figure 2). We tested whether density observed from aircraft are also lower in these areas. Because observation conditions may have differed in the two areas, we included sea state as a second factor in a two-way ANOVA. Mean values are presented in Table 3. For 1984, three categories of sea state were used: Beaufort 0 & 1, Beaufort 2, and Beaufort 3 and greater. The effect due to area was significant ($P < 0.001$), with the area that showed low density in the ship surveys also showing lower density in the aerial survey. For 1985, only the first two categories of sea state were used due to insufficient data at Beaufort 3 and greater. Again the effect of area was significant ($P < 0.025$), and the same trends were seen. In neither case were the effects of sea state or the interaction effects significant. To eliminate area effects from confounding statistical results, only data for the larger, high-density area were included in subsequent tests. The low-density area was included in later estimates of overall harbor porpoise density.

TABLE 3.—Uncorrected harbor porpoise densities (km$^{-2}$) for the two-way comparison of area and sea state. Low-density areas refer to two regions in California that were found to have much lower than average density in previous ship surveys (see text). High-density areas include all other regions. Only inside swaths were included. Numbers in parentheses refer to area (km$^2$) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

| | 1984 survey | | 1985 survey | |
|---|---|---|---|---|
| Beaufort sea state | Low-density area | High-density area | Low-density area | High-density area |
| 0 & 1 | 0.027<br>(183) | 0.579<br>(264) | 0.089<br>(124) | 0.762<br>(126) |
| 2 | 0.081<br>(308) | 0.312<br>(1012) | 0.089<br>(214) | 0.183<br>(425) |
| 3+ | 0.102<br>(79) | 0.191<br>(252) | [0.000]<br>(28) | [0.049]<br>(566) |

### Sea State and Cloud Cover

Both sea state and cloud cover can affect sighting conditions. Because both are affected by local weather, the effects of these are likely to be confounded. These two factors were therefore tested simultaneously in a two-way ANOVA. We considered only the inside swath and excluded the two low-density regions. We used the same sea state categories as above. The sky was categorized as clear if cloud cover was <25% and cloudy if >25%. Mean porpoise densities for each category are given in Table 4. It was necessary to exclude the Beaufort 0 & 1 category for 1985 because only 52 km were surveyed in cloudy conditions for these sea states. The effect due to cloud cover was significant for 1984 ($P < 0.025$) and 1985 ($P < 0.05$). The effect of sea state and the interaction effect of sea state and cloud cover were not significant for either survey ($P > 0.10$). Transect segments with >25% cloud cover were excluded from subsequent analyses.

TABLE 4.—Uncorrected harbor porpoise densities (km$^{-2}$) for the two-way comparison of sea state and cloud cover. Clear refers to <25% cloud cover, and cloudy refers to >25%. Data include only inside swaths in high-density areas. Numbers in parentheses refer to area (km$^2$) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

| | 1984 survey | | 1985 survey | |
|---|---|---|---|---|
| Beaufort sea state | Clear | Cloudy | Clear | Cloudy |
| 0 & 1 | 1.340<br>(81) | 0.240<br>(183) | [0.832]<br>(115) | [0.000]<br>(11) |
| 2 | 0.371<br>(572) | 0.236<br>(440) | 0.271<br>(232) | 0.078<br>(193) |
| 3+ | 0.266<br>(162) | 0.056<br>(90) | 0.088<br>(272) | 0.014<br>(294) |

### Sea State

The effect of sea state was tested alone using only the transect segments which occurred under clear skies (<25% cloud cover) and within the high-density areas. For 1984, only the inside swath was included.

For 1985, both inside and outside swaths were included. As in previous stratifications, apparent density clearly decreased with increasing sea state (Table 5). This effect was significant for surveys in both 1984 ($P < 0.05$) and 1985 ($P < 0.005$). Transect segments surveyed during sea states of 2 or greater were excluded in subsequent analyses.

TABLE 5.—Uncorrected harbor porpoise densities (km$^{-2}$) for the stratification based on sea state. Data include only high-density areas surveyed when cloud cover was <25%. Data for 1984 include inside swaths only; data for 1985 include inside and outside swaths. Numbers in parentheses refer to area (km$^2$) surveyed under the given condition.

| Beaufort sea state | 1984 survey | 1985 survey |
|---|---|---|
| 0 & 1 | 1.340<br>(81) | 0.807<br>(234) |
| 2 | 0.371<br>(572) | 0.193<br>(471) |
| 3+ | 0.266<br>(162) | 0.058<br>(553) |

## Between Survey Differences

We considered the 1984 survey and the 1985 surveys at 0.61 km and 1.85 km from shore as three independent estimates of harbor porpoise density. Because apparent density was shown to vary greatly with sighting conditions and because sighting conditions varied between surveys, it was necessary to compare these three under similar conditions.

The highest (and presumably least biased) densities were obtained when sea state was Beaufort 0 & 1 and when cloud cover was <25%. Between survey comparisons under these conditions are given in Table 6 for the eight geographic regions given in Figure 2. For 1985, there were no transect segments at 0.61 km from shore under the conditions Beaufort 0 & 1 and clear skies. For 1984, only three regions contained more than 10 km$^2$ of searching effort at 0.61 km from shore. For 1985, only four areas had any searching effort at 1.85 km from shore. The only direct density comparisons with reasonable sample sizes are for region 1 (0.000 vs. 0.048 porpoise/km$^2$) and region 3 (0.111 vs. 0.110 porpoise/km$^2$) (respectively for 1984 and 1985). The densities for all regions pooled (0.671 and 0.510 porpoise/km$^2$) are similar, but because of the small sample size and geographic variation in sampling, a statistical test of this difference is meaningless.

In comparing surveys, sample size and regional coverage improved slightly when Beaufort 2 was considered (still allowing a maximum of 25% cloud cover) (Table 7). For 1984, coverage was relatively complete in all regions. For 1985, coverage at 0.61 km from shore was limited to regions 2–4, and coverage at 1.85 km was limited to regions 1–5. Comparing the two surveys in 1985, distance from shore made little difference in overall density for all regions combined, and neither survey had consistently higher values than the other. Comparing the 1984 survey to the two 1985 surveys, the former had a higher overall density for all regions combined, but again this difference was not consistent among regions. Sample size and regional coverage were again too poor for meaningful statistical tests.

TABLE 6.—Uncorrected harbor porpoise densities (km$^{-2}$) in eight geographic regions surveyed during Beaufort 0 & 1 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km$^2$) surveyed under the given condition.

| Geographic region | 1984 survey density 0.61 km | 1985 survey density 0.61 km | 1985 survey density 1.85 km |
|---|---|---|---|
| 1 | 0.000<br>(43) | —<br>(0) | 0.048<br>(103) |
| 2 | 0.000<br>(1) | —<br>(0) | 0.609<br>(51) |
| 3 | 0.111<br>(45) | —<br>(0) | 0.110<br>(55) |
| 4 | 0.953<br>(6) | —<br>(0) | 0.862<br>(183) |
| 5 | 1.120<br>(9) | —<br>(0) | —<br>(0) |
| 6 | 1.374<br>(64) | —<br>(0) | —<br>(0) |
| 7 | 5.745<br>(1) | —<br>(0) | —<br>(0) |
| 8 | —<br>(0) | —<br>(0) | —<br>(0) |
| All regions | 0.671<br>(170) | —<br>(0) | 0.510<br>(392) |

## Ventilation Patterns

Harbor porpoise did not appear to react to the helicopter during aerial observations; they were visible throughout a surfacing series and were not visible during dives. Knowing this, we were able to use data on surfacing series and dive times to determine the fraction of time harbor porpoise would be visible from the air. Data on ventilation patterns were available from the helicopter study in California (13 groups were observed, mean group size was 2.7), the Oregon shore observations (11 groups, mean group size was 4.2), and a previous shore study in Glacier Bay, AK (28 solitary individuals). The mean times spent in surfacing series were 34.2, 24.6, and 30.0 seconds (respectively for the three studies). The corresponding mean dive times did not differ significantly between study sites ($P > 0.05$ using pairwise $t$-tests). Using the pooled data set ($n = 52$), the mean time spent in a surfacing series was 30.02 seconds (SE = 1.95) and the mean time spent in a dive was 95.81 seconds (SE = 5.32). The percentage of time spent at the surface is 23.9%.

## Average and Adjusted Density Estimates

Harbor porpoise densities under optimal conditions (Beaufort 0 & 1 and <25% cloud cover) were averaged for the two surveys, weighting by transect length (Table 8). Given an average survey speed of 160 km/h and assuming that the window for harbor porpoise observation is 400 m long, the time window during which a point would be visible is 9.0 seconds. Using this estimate and the surface and dive times estimated above, the probability that a porpoise will be seen is estimated as 0.310 from Equation (2). An instantaneous count would therefore underestimate porpoise abundance by a factor of 3.2. Average values were therefore multiplied by this factor (Table 8).

TABLE 7.—Uncorrected harbor porpoise densities ($km^{-2}$) in eight geographic regions surveyed during Beaufort 2 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area ($km^2$) surveyed under the given condition.

| Geographic region | 1984 survey density 0.61 km | 1985 survey density 0.61 km | 1985 survey density 1.85 km |
|---|---|---|---|
| 1 | 0.000<br>(107) | —<br>(0) | 0.184<br>(103) |
| 2 | 0.092<br>(109) | 0.102<br>(59) | 0.103<br>(68) |
| 3 | 0.196<br>(117) | 0.062<br>(48) | 0.287<br>(52) |
| 4 | 0.562<br>(180) | 0.282<br>(110) | 0.070<br>(57) |
| 5 | 0.489<br>(119) | 0.459<br>(6) | 0.234<br>(171) |
| 6 | 0.439<br>(57) | —<br>(0) | —<br>(0) |
| 7 | 0.114<br>(70) | —<br>(0) | —<br>(0) |
| 8 | 0.268<br>(37) | —<br>(0) | —<br>(0) |
| All regions | 0.295<br>(796) | 0.192<br>(224) | 0.188<br>(452) |

## DISCUSSION

Results indicate that sighting conditions must be very good in order to estimate harbor porpoise abundance from aerial strip transects. Both sea state and cloud cover had very large and significant effects on apparent density. Limiting observations to the best categories of sea state (Beaufort 0 & 1) and cloud cover (<25%) can be used to minimize the bias due to missed animals. These conditions are, however, rare and only occurred during 5.3% and 10.3% of the transects in 1984 and 1985. The actual occurrence of these conditions is even more rare if one considers flights that were cancelled due to bad weather.

The effects on sea state and cloud cover on sighting conditions were predicted by observers before analysis of survey data was begun. Most harbor porpoise were first seen when submerged a small distance below the surface. Surfacings were relatively inconspicuous to aerial observers and were not an important cue in sighting porpoise. Both sea state and cloud cover affect the ability of observers to see through the water's surface and to spot submerged animals. Increasing sea state causes more refraction of light at the water's surface, increases glit-

TABLE 8.—Harbor porpoise densities ($km^{-2}$) in eight geographic regions from a) a weighted average of uncorrected estimates from 1984 and 1985 aerial surveys, b) the same average adjusted by a factor of 3.2 to account for submerged porpoise that were missed by aerial observers, and c) a weighted average for the 1984 and 1985 ship surveys. Aerial estimates are based on observations made under conditions of Beaufort 0 & 1 and with <25% cloud cover. Ship estimates include Beaufort sea states of 0, 1, and 2.

| Geographic region | Area surveyed ($km^2$) | Aerial estimates Uncorrected a | Aerial estimates Corrected b | Research vessel estimates c |
|---|---|---|---|---|
| 1 | 146 | 0.03 | 0.10 | 0.05 |
| 2 | 1 | — | — | 0.66 |
| 3 | 100 | 0.11 | 0.35 | 0.04 |
| 4 | 189 | 0.86 | 2.75 | 3.68 |
| 5 | 9 | 1.12 | 3.58 | 1.18 |
| 6 | 64 | 1.37 | 4.38 | 2.88 |
| 7 | 1 | — | — | 3.43 |
| 8 | 0 | — | — | 1.42 |
| All regions | 562 | 0.559 | 1.79 | 1.73 |

tery reflection of sunlight, and causes whitecaps which obscure subsurface observation. Cloud cover decreases penetration of sunlight into the sea and causes its surface to appear dark and glazed. It is therefore not surprising that calm seas and clear skies result in higher apparent densities.

It is more surprising that apparent density did not vary with observer's subjective appraisal of surface penetration. This may have been because surface penetration was only tested in paired cases for which sea state and cloud cover were identical. In these cases, differences in surface penetration may have been due primarily to subjective differences in the way individual observers were coding it. If all cases are considered, surface penetration is very highly correlated with sea state and cloud cover and probably could be used as an alternative measure of sighting conditions. We prefer, however, to use sea state and cloud cover because their measure is less subjective than surface penetration and could more easily be used by other researchers.

### Missed Animals

A principal assumption of strip transect methods is that all individuals within the strip are counted. We cannot necessarily meet this assumption just by eliminating the categories of sighting conditions with significantly lower density. In fact, it is possible that this method of selectively eliminating data could overestimate density by eliminating a category of sighting conditions which (by random chance) had a significantly lower density. We do not believe that this is likely in the cases of sea state or cloud cover because the trends were the same for both surveys and because the categories that were eliminated were judged a priori as being poorer sighting conditions. We believe that porpoise density is more likely underestimated due to missed animals. Kraus et al. (1983) found that observers in aircraft saw only 14% of the harbor porpoise groups known to be present based on shore-based observations. Missed animals may include some individuals that were near the surface and visible but were not seen, as well as others that were diving and were too deep to be seen.

We infer that some near-surface animals were missed based on three reasons. First, apparent density decreased with increasing sea state and cloud cover, hence near-surface animals must be missed in (at least) the poorer conditions. (An alternative explanation is that porpoise spend less time near the surface when sighting conditions are poor.) Second, of the two principal observers in 1985, the less experienced observer may have missed more porpoise. Third, in five instances in 1984 and one instance in 1985, the data recorder saw harbor porpoise in the inside swath that were missed by the observer. In three of these cases, conditions were Beaufort 1 with <25% cloud cover. Recorders searched only occasionally as conditions permitted, so it is not possible to use these data to quantify how many near-surface animals were missed under good conditions.

Based on behavioral observations, we can also be certain that some harbor porpoise are missed because they are too deep to be seen. Water visibility was typically only 2–5 m during the surveys. Aerial observers have seen harbor porpoise dive out of view during the passing of the plane or while circling. Harbor porpoise were not visible from the helicopter during dives, even in very calm water. Some fraction of porpoise must be missed because they are too deep to be seen.

We have tried to account for the fraction of diving animals by dividing density estimates by the fraction of time harbor porpoise are known to be near the surface (i.e., within surfacing series). Uncorrected estimates of harbor porpoise density are based on the assumption that porpoise are never too deep to be seen; this undoubtedly results in an underestimate of porpoise density. Our method of adjusted estimates of porpoise density assumes that, when diving, porpoise are always too deep to be seen; this has been corroborated by helicopter observations. The latter estimate should therefore be closer to the true value of porpoise density (if biases due to other factors have been eliminated).

### Offshore Distribution of Harbor Porpoise

In 1985, aerial transects were flown at 0.61 and 1.85 km from the shore. The latter value was chosen to correspond approximately to the ship transects along the 10-fathom (18.3 m) isobath. The intent was to directly compare aerial estimates of density to estimates made from ships at the same distance from shore (considered below) and to provide a means to extrapolate ship estimates to regions that were too shallow to survey by ship. In regard to the latter, we wish to know whether harbor porpoise density at 0.61 km from shore is different from that at 1.85 km.

In 1985, surveys at 0.61 km were never flown under good sighting conditions (Beaufort 0 & 1 and <25% cloud cover), so direct comparisons between 0.61 and 1.85 km are not possible. Considering only the best category of sighting conditions, it is possible to compare 1985 transects at 1.85 km with 1984 transects at 0.61 km in geographic regions 1 and 3 (Table 6). Sample sizes are very small, but densities are roughly comparable (0.070 vs. 0.057, respectively for 1.85 and 0.61 km from shore). Sample sizes in 1985 can be increased if Beaufort 2 is considered instead of Beaufort 0 & 1 (still with <25% cloud cover). Based on geographic regions 1 through 5, porpoise densities are virtually identical at 1.85 and 0.61 km from shore (0.188 vs. 0.192, respectively, Table 7).

In a preliminary model of harbor porpoise depth distribution, Barlow (1988) hypothesized that harbor porpoise density is constant from the shore to the 75 m isobath. Ship data did not, however, include any transects inshore of 18.3 m depth. In this shallow area, the model was not based on any data. Although sparse, data from aerial surveys show that densities are similar in areas that were surveyed by ship (1.85 km from shore) and in areas that were too shallow to be surveyed by ship (0.61 km from shore). These data are consistent with the model proposed by Barlow.

### Comparison of Ship and Aerial Density Estimates

Estimates of harbor porpoise density from 1984 to 1985 ship surveys (Barlow 1988) can be compared with adjusted and unadjusted estimates from the aerial surveys (Table 8). The overall density for all regions is higher for the ship surveys than for the unadjusted aerial. Adjusted estimates from the aerial surveys are very close to the overall estimates from ship surveys.

Previous comparisons have been made of sighting efficiency from aerial and surface vessel platforms (Kraus et al. 1983). They found that observers on boats saw 52% of the harbor porpoise groups seen by shore-based observers, whereas aerial observers saw only 14%. Based on this, density from aerial surveys might be expected to be only 27% of that from ship surveys. In the present study, unadjusted density based on aerial surveys is 32% of the density from ship surveys. The two studies are not directly comparable, however. Weather conditions are not reported by Kraus et al. (1983) and may have included less than optimal sighting conditions. It should be noted that the fraction of harbor porpoise groups seen by aerial observers in their study (14%) is even lower than the fraction of harbor porpoise we assumed would be in surfacing series and hence near the surface (23.9%). It is possible that behavioral differences between harbor porpoise from the two coasts (such as travelling or behavior mode "A" noted by Watson and Gaskin (1983)) could account for some of the differences noted above.

Estimates based on ship surveys cannot, of course, be considered the true density of harbor porpoise. The overall estimate based on ship surveys is relatively imprecise (C.V. = 49%) and may be biased (Barlow 1988). The ship survey estimate is, however, superior to current estimates from aircraft for several reasons. Line transect methods were used on the ship surveys, and the principal assumption of this method (that 100% of the animals in the immediate vicinity of the trackline are seen) is more easily met than the comparable strip transect assumption (that 100% of the animals within a strip are seen). Acceptable sighting conditions for ship surveys included Beaufort 0 & 1, and 2 and were not restricted by cloud cover (Barlow 1988). This allowed more complete geographic coverage than did aerial surveys. Also, the ship travelled much slower than the aircraft (10 knots vs. 80–90 knots), thus the probability of missing a diving individual was much less. Barlow (1988) calculated that diving animals located near the trackline would be missed by observers on ships only if dive times exceeded 2 minutes. Finally, estimates of the correction factor to account for submerged animals is relatively imprecise. Additional observations on ventilation patterns may allow further refinements in density estimates based on aerial surveys.

## RECOMMENDATIONS

The design of future surveys for harbor porpoise could be improved based on the results obtained from our aerial surveys. We found that sighting conditions deteriorated rapidly with both increasing cloud cover and rougher sea states. To the extent that is possible, aerial surveys for harbor porpoise should only occur on clear days with little wind. Observations made by the data recorders indicate that some harbor porpoise will be missed even in good sighting conditions. If strip transects are used, experiments with two independent teams of observers searching at the same time could be used to quantify the fraction of animals that are missed by using just one team. Given that fewer harbor porpoise were seen between 400 and 500 m of the track line, we also suggest that, when surveying at 213 m altitude, the strip widths should be decreased to only include the area between 100 and 400 m.

We believe, however, that the problem of missing harbor porpoise could be reduced if line transect methods were used in place of strip transects. Line transect methods assume that 100% of all animals are seen directly along the trackline and use statistical techniques to estimate the number of animals that are missed as a function of the distance from this trackline. Line transects would require use of an aircraft with unobstructed downward visibility through a belly window and use of a third observer who could view animals directly under the aircraft.

Harbor porpoise are now known to occur further from the shoreline than was believed at the beginning of this study (Barlow 1988). In future surveys, transect lines should be placed so as to cover a greater fraction of the harbor porpoise habitat.

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## LITERATURE CITED

BARLOW, J.
1988. Harbor porpoise *Phocoena phocoena*, abundance estimation for California, Oregon and Washington: I. Ship surveys. Fish. Bull., U.S. 86:417–432.

KRAUS, S. D., J. R. GILBERT, AND J. H. PRESCOTT.
1983. A comparison of aerial, shipboard, and land-based survey methodology for the harbor porpoise, *Phocoena phocoena*. Fish. Bull., U.S. 81:910–913.

KRUSKAL, W. H., AND W. A. WALLIS.
1952. Use of ranks in one-criterion analysis of variance. J. Am. Stat. Assoc. 47:583–621.

SCHEIRER, C. J., W. S. RAY, AND N. HARE.
1976. The analysis of ranked data derived from completely randomized factorial designs. Biometrics 32:429–434.

SEBER, G. A. F.
1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y., 506 p.

TAYLOR, B. L., AND P. K. DAWSON.
1984. Seasonal changes in density and behavior of harbor porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. Rep. int. Whaling Comm. 34:479–483.

WATSON, A. P., AND D. E. GASKIN.
1983. Observations on the ventilation cycle of the harbour porpoise *Phocoena phocoena* (L.) in the coastal waters of the Bay of Fundy. Can. J. Zool. 61(1):126–132.

WILCOXON, F.
1945. Individual comparisons by ranking methods. Biom. Bull. 1:80–83.

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# AN APPROACH TO RECRUITMENT RESEARCH IN INSULAR ECOSYSTEMS

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ABSTRACT: Population maintenance of species with pelagic larvae in island systems is poorly understood, but general agreement has emerged in recent years that processes in the plankton are responsible for recruitment variability. An initial, multi-disciplinary approach is suggested to examine questions of population maintenance with special attention to retention of larval forms around islands. Intensive but directed studies of physical and biological oceanography in waters surrounding an island and studies of fish populations, including recruitment patterns on the island, are proposed. A rationale is developed for the initial study to be conducted at an isolated, oceanic island to simplify the survey work and interpretation of results. Such a study could lead to new insights on the planktonic processes which affect recruitment variablity and would be invaluable to the design of similar studies in more complicated archipelagic or tropical coastal systems.

## 1. INTRODUCTION

Marine organisms which inhabit isolated islands or seamounts are faced with limited adult habitat and with ocean currents which advect larvae away from the source population; some species have probably developed mechanisms for population maintenance, but these remain largely unknown at the present time. Thus the problems of recruitment of island and seamount resources differ significantly from those of species associated with continental shelf and slope regions, regardless if in boreal, temperate, or tropical regions. In this paper I consider some of the questions which must be addressed if we are to better understand the process of recruitment in island and seamount ecosystems.

The vast majority of tropical marine species, particularly those of commercial importance, are characterized by a life history with a pelagic larval stage. While early studies typically suggested that these stages were adaptive for dispersal (Ekman,1953), an alternate view was developed by Johannes (1978), who argued that pelagic larvae were an adaptation to minimize predation of the vulnerable larval stages. Still, other scientists hold to the concept that dispersal remains the selective advantage of a pelagic stage (Barlow, 1981).

To understand recruitment in insular ecosystems, the above issue is important but the fact remains that pelagic larvae must return to replenish the source population. Several early studies of reef fish ecology held that space, rather than recruitment, was the limiting factor to these populations (Smith and Tyler 1972, 1975), inferring that a large pool of potential recruits could fill space on the reef at any time. If this were indeed the case, fishery exploitation of a given population size could possibly be maintained at a higher level than if recruitment were variable and the limiting factor. Unfortunately, more detailed study has shown that recruitment is highly variable within species. On a short time scale, Victor (1982) has shown sporadic recruitment despite continuous spawning in the labrid Thalassoma bifasciatum. Other studies have further demonstrated that recruitment is one of the most important factors in the population dynamics of reef fishes (Doherty, 1983; Williams,1983; Sale and Douglas 1984). The temporal component of recruitment variability is probably the most important, with interannual differences of at least an order of magnitude (Shulman 1985). Spatial variations, at least on the scales examined, would appear to be less important. Similar recruitment patterns may occur over scales of 1 km (Shulman,1985) to 50 km, the latter apparently after mixing of cohorts in the plankton (Victor, 1984). Eckert (1984), however, noted little similarity in spatial recruitment patterns in a series of reefs in the Great Barrier Reef system, and Sale et al. (1984) suggested that spatial variability on this scale is as important as variability in year class strength. The question of spatial variations and its relationship with temporal variability needs more work.

Since the source of variability in recruitment occurs in the planktonic stage (Victor,1983; Warner,1984) this is an important place to begin investigations. The important processes to address initially must be whether variability in recruitment is under physical or biotic control. If the pelagic larval stage is an adaptation to reduce predation as suggested by Johannes (1978), then biotic effects in the planktonic environment may not result in a strong component of interannual variability. Planktonic prey of fish larvae may be enhanced on the mesoscale by the "island mass effect" (Gilmartin and Relevante,1974) and the associated higher standing stocks of plankton near islands (Jones,1962). Physical factors, on the other hand, may play a more important role in recruitment variability. Physical oceanography around islands is complex and variable (Barkley,1972; Hogg et al.,1978; Pingree and Maddock,1980, 1985) and advection likely plays the dominant role in variability in recruitment strength in tropical island species. In the life history, biotic factors may play the dominant role after settlement.

## 2. MECHANISMS OF POPULATION MAINTENANCE

The physical mechanisms important in larval retention around islands, banks, or seamounts have been discussed by Bakun (this volume) and I will not elaborate on them here. The physical processes alone, however, are not likely to result in retention of larvae; related biological processes, such as temporal spawning activity by adults and behavioral attributes of the planktonic stages, doubtless interact with the physical mechanisms to result in retention and ultimate recruitment (Lobel and Robinson,1983). While flow patterns may result in significant aggregation of planktonic organisms under certain situations (Hamner and Hauri, 1981), insular holoplanktonic assemblages distinct from oceanic assemblages occur around islands and patterns of convergences may maintain such populations (Boden,1952). Peterson et al. (1979) described a similar mechanism for maintenance of a copepod population in an upwelling area, but invoked a behavioral mechanism to explain differential utilization of current patterns. Larvae are capable of significant behavioral responses to physical factors which may result in alterations in the distribution pattern (Boehlert and Mundy, 1986).

Eddies and gyres which form around islands and seamounts may act to trap waters for significant periods of time (Pingree and Maddock,1980; Wolanski et al. 1984). Sale (1970), Emery (1972), and Shomura and Barkley (1979) suggested that such eddies were important in retaining planktonic stages. Further conceptual development of this idea has been provided by Lobel and Robinson (1983); data supporting the role of eddies in population maintenance exist for the continental shelf off Norway (Sundby,1984), Rockall Bank (Dooley,1984), and George's Bank (Smith and Morse,1985). Understanding the physical and temporal attributes of such eddies will be necessary to show their importance in a recruitment mechanism.

## 3. CURRENT RESEARCH APPROACHES

The study of recruitment has historically taken indirect approaches which look at the final result, including age distributions, year class strengths, and, in the case of reef fishes, temporal and spatial recruitment patterns, looking at the results of the process of recruitment rather than the mechanism. Many of the recent studies outlined above demonstrate significant temporal variability in recruitment, including interannual variability, despite a relatively stable spawning stock. The work of Victor (1983, 1984), in particular, points to processes in the plankton which determine the timing and strength of recruitment in tropical systems (Warner, 1984). The northern anchovy in the California Current system was studied for many years as part of the CalCOFI program and this historical data base on larval distribution and abundance has been critical to further work; the greatest advances in understanding causes of recruitment success or failure, however, have been made in the last decade by determining the role of physical (storms, turbulence) and biotic (prey microdistribution) factors (Lasker 1975, 1978) and their effects on mortality in the field. This approach has allowed generalities to be drawn about similar ecosystems (Bakun, 1985). A comparative approach could also be profitable in tropical systems.

Much of the research on recruitment in tropical fishes has addressed the issue of the high diversity of reef fishes (Sale, 1982), but recent studies on recruitment have directed more researchers to look to processes in the plankton as determinants of recruitment (Helfman, 1978; Doherty et al. 1985; McFarland and Ogden, 1985). Studies on the reef have documented spawning activity and recruitment patterns, but little research has been done on the intervening pelagic stage (McFarland and Ogden, 1985). Still, research on the growth patterns of recruits has resulted in a greater understanding of the timing and variability of recruitment. Use of daily growth increments on new recruits and the ability to detect "recruitment marks" on older ones (Ralston, 1975; Brothers and McFarland 1979) has led to inferences regarding age at recruitment for many species (Brothers and Thresher, 1985; Brothers et al. 1983). Application of this technique to a single species has shown a high degree of spatial coherence in recruitment pattern over a scale of 50 km in the Caribbean (Victor, 1984); this study was significant in that the ages within groups recruiting at the same time were mixed, suggesting that cohorts spawned at different times were mixed in the plankton. These studies are important and allow us to draw inferences about processes occurring in the planktonic environment.

There have been fewer studies in the pelagic environment in tropical ecosystems which relate to recruitment. Distributional studies have typically lacked the detailed physical measurements necessary to understand the meaning of observed patterns. Several intriguing results nonetheless exist. Miller (1974), for example, noted differences in abundance of fish larvae upstream, downstream, and in the reef waters of Molokini, a small islet near Maui in Hawaii; larval fish in reef waters and downstream were typically smaller than in upstream waters, but were 26 and 4 times as abundant, respectively. It is known that areas of stagnant water may be held in the lee of islands in response to a current (Pingree and Maddock, 1980; Wolanski et al. 1984) and that zooplankton may swarm or form aggregations in such locations (Hamner and Hauri, 1981). An interesting point of Miller's study, however, was that densities of passively transported tunicate eggs did not differ among the three areas, suggesting that larval behavior was an important feature of the observed distributional patterns. Other studies in Hawaii have documented differences in distributional patterns among different groups of ichthyoplankton (Leis and Miller, 1976; Leis 1982b); Leis (1982a) has also used eggs and larvae of nearshore species as tracers of coastal water but later suggested that "the assumption that larvae of reef fishes are passive particles to be treated as conservative properties of water parcels is unjustified without much more information than is currently available on larval behavior" (Leis and Goldman, 1984). While these studies provide intriguing results, they lack the concurrent physical data necessary for firm interpretation. More recent studies on small reefs within the Great Barrier Reef have included physical measurements (Leis and Goldman, 1983, 1984; Williams et al. 1984).

## 4. AN APPROACH TO UNDERSTANDING INSULAR RECRUITMENT MECHANISMS

Components of a fairly comprehensive program addressing insular recruitment in the Caribbean were discussed in Richards (1982) and included studies of physical oceanography, larval distribution, planktology, primary productivity, and fisheries data analysis. In this paper I recommend a more modest approach for an initial but intensive study. If we agree that processes in the plankton are the major source of variability in recruitment, then we narrow the primary sources of this variability to either physical (advection) or biotic (predation, prey availability) factors (Hunter, 1976). While the biotic factors doubtless play a role, study of predation- or starvation-induced mortalities may be premature in tropical ecosystems, mainly because our understanding of distributional patterns is somewhat rudimentary and abundances of shore-fish larvae are quite low (Leis and Miller, 1976). Reef fishes typically have extended spawning seasons and apparently use a planktonic stage to reduce predation on the reef (Johannes, 1978; Thresher and Brothers, 1985); also, species with planktonic eggs may spawn in a manner which minimizes temporal and spatial overlap with predators (Frank and Leggett, 1985). Although predation may be an important source of interannual variability in mortality of larval stages, it will be difficult to study without knowledge of distribution. Advection and other physical factors may initially be a more tractable problem for study and clearly play an important role in recruitment variability in tropical island ecosystems. While not intensively studying prey and predator distribution, an initial study of advection, distribution, and retention mechanisms would provide preliminary distributional data which could later be used to design studies of prey microscale distribution (Owen, 1981) or predation and starvation (Hewitt et al. 1985).

Another way to simplify an initial tropical recruitment experiment would be to conduct the work around an isolated, oceanic island. This provides two advantages. First, the complexities in physical oceanography inherent in archipelagic systems, including eddies and downstream effects, will be minimized (Barkley, 1972). Secondly, it avoids the problem of an unknown source population. Early larvae and the vast majority of recruits of shore fishes captured near an isolated oceanic island were likely spawned there. Shore-based studies of recruitment (Victor, 1982, 1984; McFarland et al. 1985; Shulman, 1985) have typically not addressed the problem of the source of recruits. With a pelagic duration of 20-50 days (Brothers and Thresher, 1985), recruits could come from a wide geographic area. Remaining in an isolated system for an initial experiment thus has the advantage of providing a better understanding of the primary mechanisms involved in larval retention and recruitment which may then be applied to more complicated systems; it also will address the question of locally recruiting populations proposed by Bakun (this volume). Another advantage is that the populations may be unexploited and thus population characteristics such as age distribution and natural mortality can be determined from sampling and age analysis.

The proposed study would involve physical and biological components. The physical oceanographic component would involve primarily measurements of mesoscale phenomena, first looking at the general geostrophic flow component and its variability and studying the effects of the island on flow, including both local and downstream effects. Specifically, the physical retention mechanisms considered in Bakun (this volume) must be evaluated to assess their ability to retain larvae and juveniles in the region of the island. In the initial, intensive studies, special consideration should be given to developing simpler means of determining flow patterns, including use of XBT data, perhaps in conjunction with objective analysis models (Mooers and Robinson,1984), should they prove reliable in waters around islands. Special attention should also be paid to remote sensing methods. Surface thermal images in the tropics may not be of great value, but ocean color analysis can be used to detect variations in chlorophyll which might be related to island effects (Dandonneau and Charpy, 1985). Similarly, satellite altimetry could potentially be used for detection of eddies or current patterns and may facilitate subsequent detection of the appropriate signals.

The biological program in offshore waters will be primarily shipboard sampling and should concentrate on local island species. Sampling for variability in abundance and microdistribution of prey, primary productivity, and other trophic factors would be minimized in this initial study. Patterns of chlorophyll distribution, however, should be taken to ground-truth remote sensing proposed for the physical component. Initially, a large scale spatial study of larval and juvenile fish distribution will be necessary, including upstream/downstream sampling and intensive sampling in the island wake region and nearshore waters. As an example, preliminary data on horizontal ichthyoplankton abundance around Johnston Island (Figure 1) demonstrate that larval abundance in downstream waters may be several times higher than in upstream waters; the increases are explained by increases of shore-fish larvae as opposed to midwater or noninsular forms. Unfortunately, concurrent physical data are unavailable from this study to test the retention mechanisms proposed by Bakun (this volume). Limited sampling should also be conducted in the shallows or lagoon waters, but these have not typically been shown to be important nurseries for most species (Leis, 1981; Leis and Goldman 1983). The ichthyoplankton sampling should be conducted with high resolution in the vertical plane, with concurrent sampling of physical factors (depth, temperature, salinity) as is done with the MOCNESS or BIONESS nets. Scoping studies should be done to determine the depths of residence of shore fish larvae and these depths should be studied intensively to minimize the needed sampling; typically, the upper mixed layer is where the majority of shore fish larvae will be found in tropical systems, as shown for waters off Hawaii (Figure 2). Studies of the relationship of larval distribution to physical and diel factors can then be used to infer behavioral patterns and their role in the physical retention mechanisms.

Larger volume sampling techniques, particularly midwater trawls, should be used to define the horizontal patterns of larger larvae and transformed juveniles which are rare or undersampled by the plankton gear; to maximize the use of shiptime, large nets as described in Pearcy (1980) which are semi-quantitative and have uniform mesh, should be used. Such large sampling gear was used by Sale (1970), who observed overall densities of juvenile convict surgeonfish, *Acanthurus triostegus*, of 0.0017 per 1000 $m^3$. Although these densities are low, such nets may sample 100 $m^3$ per second when towed at 2 kt and thus detect areas of moderate density with reasonable sampling times.

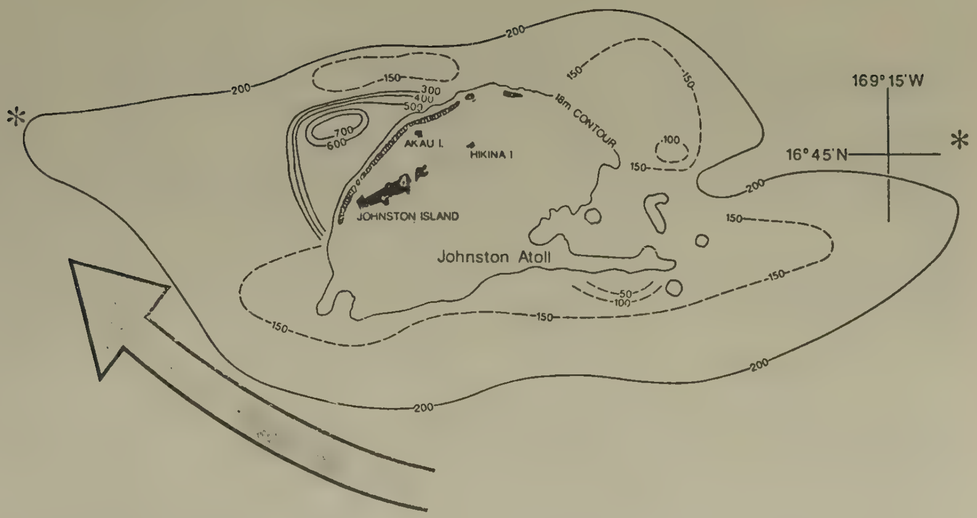

FIGURE 1. Distribution of ichthyoplankton around Johnston Island in November, 1984 collected from the *Townsend Cromwell* with a 1 $m^2$ opening-closing Tucker trawl. Densities refer to numbers of larvae per $10^3$ $m^3$ in the 50-100 m depth stratum. The arrow represents surface current deduced from drogues deployed a month earlier (P. S. Lobel, personal communication). Note the high density of larvae on the downstream side of the island. Data from Boehlert (unpublished). Asterisks indicate that collections were made at greater distances east and west of the atoll.

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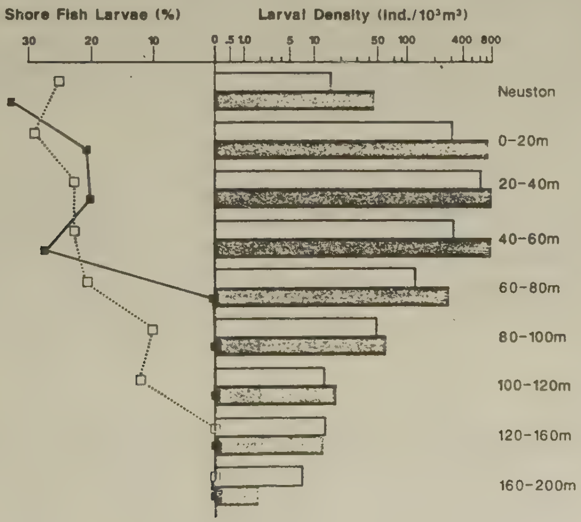

FIGURE 2. Larval densities (log scale) as a function of depth at both day and night at a station 5 nmi off the leeward coast of Oahu, Hawaii (lat. 21°21' N., long. 158°13.3' W.) taken in September, 1985. Each value represents a single haul. Clear bars represent day densities, cross-hatched bars represent night densities. The neuston samples are from the surface to 70 cm. On the left of the figure, the percentage of shore fish larvae (as opposed to pelagic or midwater fishes) is shown, with closed squares representing night, open squares day samples. Data from Boehlert and Mundy (unpublished).

A nearshore biological component of this study should be developed to sample all life stages from new recruits to adults. The age structure of adult populations should be determined with sufficient numbers to allow both estimation of mortality rates and variability in year class strength. These should be combined with length-based methodologies to streamline subsequent sampling. Sampling of new recruits should be undertaken during and after the main offshore sampling. This part of the study should at least include surveys to assess the densities of recruits and otolith studies to determine the birthdate and settlement date distribution of recruits. This will provide both the planktonic duration and the success of cohorts sampled during earlier offshore work. The latter work would be particularly important to correlate with physical oceanography and the distribution and abundance of earlier life stages in the pelagic environment.

From a temporal standpoint, the intensive study should be conducted during the season which coincides with the spawning peaks of most reef species, but preferably for a longer period in the first year to assess seasonal variability. The duration of the intensive offshore study should be at least one month, which will allow the distributional and physical analysis as well as coinciding with the approximate pelagic duration of many fish species (Brothers and Thresher, 1985). This type of study should be conducted over a period of two or three years (with more precise and therefore less intensive sampling each year) to assess interannual variability. If remote sensing methods prove useful, relevant data could be collected throughout the year.

This study should concentrate on any insular species to allow flexibility. Target species attributes should include known life histories (identified larvae, juvenile stages and habitats), sufficient larval and juvenile abundance to statistically assess distributional patterns and recruitment, and a large enough adult population to allow repeated sampling and estimation of population age structure. As with any ichthyoplankton program, however, the proposed research should consider the suite of species captured in the study to evaluate species associations.

If framed as a two to three year study, this research could provide answers to many unanswered questions about recruitment in tropical insular ecosystems. The study of an isolated island ecosystem would provide focused hypotheses which could then be tested in the more complicated archipelagic and island group systems where fisheries for a variety of species with pelagic eggs and larvae exist. To achieve these objectives, however, an intensive and interdisciplinary approach will be necessary.

## 5. REFERENCES

Bakun, A. (1985) Comparative studies and the recruitment problem: Searching for generalizations. Calif. Coop. Oceanic. Fish. Invest., Rep., 26:30-40.

Barlow, G. W. (1981) Patterns of parental investment, dispersal and size among coral-reef fishes. Environ. Biol. Fishes, 6:65-85.

Barkley, R. A. (1972) Johnston Atoll's wake. J. Mar. Res., 30:201-216.

Boden, B. P. (1952) Natural conservation of insular plankton. Nature, 169: 697-699.

Boehlert, G. W. & B. C. Mundy (1986) The role of behavioral and physical factors in fish recruitment to estuarine nursery areas. *Trans. Am. Fish. Soc.* (In press).

Brothers, E. B. & W. N. McFarland (1979) Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts [*Haemulon flavolineatum* (Desmarest), Haemulidae]. *Rapp. P.-V. Réun. Cons. int. Explor. Mer*, *178*:369-374.

Brothers, E. B. & R. E. Thresher (1985) Pelagic duration, dispersal, and the distribution of Indo-Pacific coral reef fishes. In: *The Ecology of Coral Reefs*, editors M. L. Reaka, *NOAA Symp. Ser. Undersea Res.* Vol., *3*, p. 53-70.

Brothers, E. B., D. M. Williams & P. F. Sale (1983) Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. *Mar. Biol.* (*Berl.*), *76*:319-324.

Dandonneau, Y. & L. Charpy (1985) An empirical approach to the island mass effect in the south tropical Pacific based on sea surface chlorophyll concentration. *Deep-Sea Res.*, *29*:953-965.

Doherty, P. J. (1983) Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology*, *64*:176-190.

Doherty, P. J., D. M. Williams & P. F. Sale (1985) The adaptive significance of larval dispersal in coral reef fishes. *Environ. Biol. Fishes*, *12*:81-90.

Dooley, H. D. (1984) Aspects of oceanographic variability on Scottish fishing grounds. Ph.D. Thesis, Univ. Aberdeen, Scotland, 154 p.

Eckert, G. J. (1984) Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker Group, Great Barrier Reef. *Mar. Biol.* (*Berl.*), *78*:123-127.

Ekman, S. (1953) *Zoogeography of the sea.* Sidgwick and Jackson, London, 417 p.

Emery, A. R. (1972) Eddy formation from an oceanic island: ecological effects. *Caribb. J. Sci.*, *12*:121-128.

Frank, K. T. & W. C. Leggett (1985) Reciprocal oscillations in densities of larval fish and potential predators: A reflection of present or past predation. *Can. J. Fish. Aquat. Sci.*, *42*:1841-1850.

Gilmartin, M. & N. Relevante (1974) The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *J. Exp. Mar. Biol. Ecol.* *16*:181-204.

Hamner, W. M. & I. R. Hauri (1981) Effects of island mass: Water flow and pattern around a reef in the Great Barrier Reef lagoon, Australia. *Limnol. Oceanogr.*, *26*:1084-1102.

Helfman, G. S. (1978) Patterns of community structure in fishes: Summary and overview. *Environ. Biol. Fishes*, *3*:129-148.

Hewitt, R. P., G. H. Theilacker, and N. C. H. Lo (1985) Causes of mortality in young jack mackerel. *Mar. Ecol. Prog. Ser., 26*:1-10.

Hogg, N. E., E. J. Katz & T. B. Sanford. (1978) Eddies, islands, and mixing. *J. Geophys. Res. 83*(C6):2921-2938.

Hunter, J. R. Editor (1976) Report of a colloquium on larval fish mortality studies and their relation to fishery research, Jan. 1975. U.S. Dep. Commer., *NOAA Tech. Rep. NMFS Circ-395*, 5 p.

Johannes, R. E. (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environ. Biol. Fishes, 3*:65-85.

Jones, E. C. (1962) Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Islands, Central Pacific. *J. Cons. int. Explor. Mer, 27*:223-231.

Lasker, R. (1975) Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull., U.S., 73*:453-462.

Lasker, R. (1978) The relation between oceanographic conditions and larval anchovy food in the California current: Identification of factors contributing to recruitment failure. *Rapp. R.-V. Réun. Cons. int. Explor. Mer, 173*:212-230.

Leis, J. M. (1981). Distribution of fish larvae around Lizard Island, Great Barrier Reef: Coral reef lagoon a refuge? *Proc. 4th Int. Coral Reef. Symp.* Manila. Vol. *2*, p. 471-477.

Leis, J. M. (1982a) Hawaiian creediid fishes (*Crystallodytes cookei* and *Limnichthys donaldsoni*): Development of eggs and larvae and use of pelagic eggs to trace coastal water movement. *Bull. Mar. Sci., 32*:166-180.

Leis, J. M. (1982b) Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. *Mar. Biol. (Berl.), 72*:89-97.

Leis, J. M. & B. Goldman (1983) Studies of the biology of larvae fishes in the Lizard Island area, northern Great Barrier Reef. In: *Proceedings of the Inaugural Great Barrier Reef Conference*, p. 221-225, Townsville, editors J. T. Baker, R. M. Carter, P. W. Sammarco, and R. P. Stark, James Cook Univ. Press, Townsville.

Leis, J. M. & B. Goldman (1984) A preliminary distributional study of fish larvae near a ribbon coral reef in the Great Barrier Reef. *Coral Reefs, 2*:197-204.

Leis, J. M. & J. M. Miller (1976) Offshore distributional patterns of Hawaiian fish larvae. *Mar. Biol. (Berl.), 36*:359-367.

Lobel, P. S. & A. R. Robinson (1983) Reef fishes at sea: ocean currents and the advection of larvae. In: *The Ecology of Deep and Shallow Coral Reefs, Symp. Ser. Undersea Res.*, editor M. L. Reaka, *NOAA Undersea Res. Prog.* Vol. *1*, No. 1, p. 29-38.

McFarland, W. N., E. B. Brothers, J. C. Ogden, M. J. Schulman, E. L. Bermingham N. M. Kotchian-Prentiss (1985) Recruitment patterns in young French grunts, *Haemulon flavolineatum* (Family Haemulidae), at St. Croix, Virgin Islands. *Fish. Bull., U.S.*, *83*:413-426.

McFarland, W. N. & J. C. Ogden (1985) Recruitment of young coral reef fishes from the plankton. In: The Ecology of Coral Reefs, editor M. L. Reaka, *NOAA Symp. Ser. Undersea Res.*, Vol. *3*, p. 37-52.

Miller, J. M. (1974) Nearshore distribution of Hawaiian marine fish larvae: effects of water quality, turbidity and currents. In: *The Early Life History of Fish*, editor J. H. S. Blaxter, Springer Verlag, New York, p. 217-232.

Mooers, C. N. K. & A. R. Robinson (1984) Turbulent jets and eddies in the California Current and inferred cross-shore transports. *Science*, *223*:51-53.

Owen, R. W. (1981) Microscale plankton patchiness in the larval anchovy environment. *Rapp. P.-V. Réun. Cons. int. Explor. Mer*, *178*:364-368.

Pearcy, W. G. (1980) A large, opening-closing midwater trawl for sampling oceanic nekton, and comparison of catches with an Isaacs-Kidd midwater trawl. *Fish. Bull., U.S.*, 78:529-534.

Peterson, W. T., C. B. Miller A. Hutchinson (1979) Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep-Sea Res.*, *26A*:467-494.

Pingree, R. D. & L. Maddock (1980) The effects of bottom friction and earth's rotation on an island's wake. *J. Mar. Biol. Assoc. U.K.*, *60*:499-508.

Pingree, R. D. & L. Maddock (1985) Rotary currents and residual circulation around banks and islands. *Deep-Sea Res.*, *32*:929-948.

Ralston, S. (1975) Aspects of the age and growth, reproduction, and diet of the millet-seed butterflyfish, *Chaetodon miliaris* (Pisces: Chaetodontidae), a Hawaiian endemic. M.S. Thesis, Univ. Hawaii, Honolulu, 102 p.

Richards, W. J. (1982) Planktonic processes affecting establishment and maintenance of reef fish stocks. In: *The Biological Bases for Reef Fishery Management*. U.S. Dep. Commer., *NOAA Tech. Memo NMFS-SEFC-80*, p. 92-102.

Sale, P. F. (1970) Distribution of larval Acanthuridae off Hawaii. *Copeia* *1970*:765-766.

Sale, P. F. (1982) Stock-recruit relationships and regional coexistence in a lottery competitive system: A simulation study. *Am. Nat.*, *120*:139-159.

Sale, P. F., P. J. Doherty, G. J. Eckert, W. A. Douglas & D. J. Ferrell (1984) Large-scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* (*Berl.*), *64*:191-198.

Sale, P. F. & W. A. Douglas (1984) Temporal variability in the community structure of fish on coral patch reefs and the relationship of community structure to reef structure. Ecology, 65:409-422.

Shomura, R. S. & R. A. Barkley (1979) Ecosystem dynamics of seamounts--a working hypothesis. In: *Proc. 4th Symp. Co-op. Study of the Kuroshio and adjacent regions*, Saikon Publ. Co., Tokyo, Japan, p. 789-790.

Shulman, M. J. (1985) Variability in recruitment of coral reef fishes. *J. Exp. Mar. Biol. Ecol.*, *89*:205-219.

Smith, W. G. & W. W. Morse (1985) Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. *Mar. Ecol. Prog. Ser.*, *24*:1-13.

Smith, C. L. & J. C. Tyler (1972) Space resource sharing in a coral reef fish community. *Nat. Hist. Mus., Los Angeles, Bull.*, *14*:125-170.

Smith, C. L. & J. C. Tyler (1975) Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. *Am. Mus. Novit.*, *2572*, 18 p.

Sundby, S. (1984) Influence of bottom topography on the circulation at the continental shelf off northern Norway. *Fiskeridir. Skr. Ser. Havunders.*, *17*:501-519.

Thresher, R. E. & E. B. Brothers (1985) Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces, Pomacanthidae). *Evolution*, *39*:878-887.

Victor, B. C. (1982) Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. *Mar. Biol.* (*Berl.*)*71*:203-208.

Victor, B. C. (1983) Settlement and larval metamorphosis produce distinct marks on the otoliths of the slippery dick, *Halichoeres bivittatus*. *In*: The Ecology of Deep and Shallow Coral Reefs, editor M. L. Reaka, *Symp. Ser. Undersea Res., NOAA Undersea Res. Prog.*, Vol.*1*, No. 1, p. 47-52.

Victor, B. C. (1984) Coral reef fish larvae: Patch size estimation and mixing in the plankton. *Limnol. Oceanogr.*, *29*:1116-1119.

Warner, R. R. (1984) Recent developments in the ecology of tropical reef fishes. *Arch. Fischereiwiss.*, *35*:43-53.

Williams, D. M. (1983) Daily, monthly and yearly variability in recruitment of guild of coral reef fishes. *Mar. Ecol. Prog. Ser.*, *10*:231-237.

Williams, D. M., E. Wolanski & J. C. Andrews (1984) Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs*, *3*:229-236.

Wolanski, E., J. Imberger & M. L. Heron (1984) Island wakes in shallow coastal waters. *J. Geophys. Res.*, *89*(C6):10553-10569.

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# Current–Topography Interactions at Mid-Ocean Seamounts and the Impact on Pelagic Ecosystems

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ABSTRACT: Ocean currents impinging on topographic obstacles such as seamounts create a high level of variability in mesoscale physical oceanography. In the N Pacific, for example, the structure of the Kuroshio and its extension differ significantly E and W of the Emperor Seamount chain, and eddy fields detected downstream may be attributed to seamount effects. Nearfield effects of seamounts have been theoretically predicted for several decades but only recently has theory been confirmed by observation. Taylor columns, quasi-stationary eddies over seamounts, alter flow patterns and thus have impacts on both benthos on seamounts and on the biota in water overlying the seamount.

SE Hancock Seamount, located at the N end of the Hawaiian Ridge (29°47'N; 179°04'E), has a summit depth of 265 m. This seamount is located near the subtropical front and is at the southerly extent of productive seamounts where trawl fisheries have existed in the past. The pelagic ecosystem in the upper 200 m over the seamount clearly differs from waters at control stations at distances of 10's of kilometers away as shown by plankton and midwater trawl hauls and hydroacoustic transects conducted during 1984 and 1985. Over the seamount, hydroacoustic transects show a significantly higher biomass of scatterers as compared to control stations. Sampling these scattering layers with small midwater trawls demonstrates high densities of a resident micronekton fauna dominated by the sternoptychid fish "Maurolicus muelleri" and the mysid "Gnathophausia longispina"; these taxa were virtually absent from the control stations, were oceanic micronekton, particularly larger forms, were generally in higher abundance than at the seamount stations. Similarly, ichthyoplankton abundance differs above the seamount and at reference stations. In summer sampling, larval fishes were less abundant over the seamount whereas in winter the abundance was greater there. The differences in distribution and abundance of both micronekton and ichthyoplankton are significant and consistently observed, suggesting that physical or biological processes at the seamount have important effects on the pelagic ecosystem. Hypotheses concerning current - topography interactions, exclusion of vertical migrators, and predation by resident micronekton and fishes can be used to explain the observed effects.

Seamounts and other areas of complex topography are frequently sites of highly productive ecosystems; the S Emperor and N Hawaiian Ridge seamounts provide a good example, with a catch of approximately one million tons of boarfish in ten years. The interaction of ocean currents and complex topography may play an important role in this high productivity, as demonstrated in the high biomass of lower trophic levels in the seamount ecosystem. Interannual variability in the latitudinal position of the subtropical front and the strength of current flow over these seamounts may result in significant differences in mesoscale physical oceanography and therefore in the productivity of these ecosystems.

## Introduction

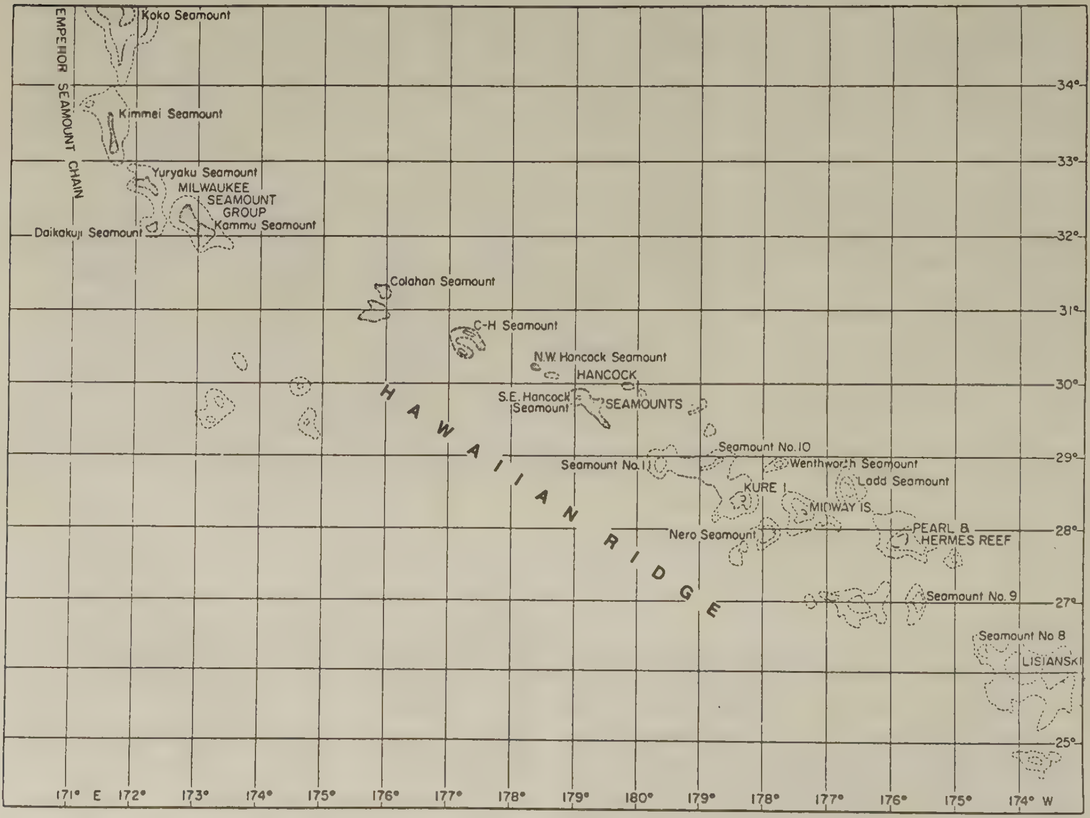
In the open ocean, seamounts interact with ocean currents to create considerable variability in the physical flow field. Several studies have described these effects on the Gulf Stream (Vastano and Warren 1976; Hurlburt and Thompson 1984) and the Kuroshio (Roden et al. 1982; Roden 1986; Darnitsky 1980b; Kozlov et al. 1982). The physical effects may spawn mesoscale eddies which alter flow patterns for significant distances downstream of the seamounts (Royer 1978). Biological effects of these physical complexities are not well understood (Boehlert 1986). Discovery of seamount fishery (Uda and Ishino 1958; Borets 1975) and mineral resources (Manheim 1986), however, has caused increased interest in seamount oceanography and its effects on biota (Bezrukov and Natarov

1976; Darnitsky et al. 1984; Genin and Boehlert 1985; Uchida et al. 1986).

The effect of sea floor topography on ocean currents has been a topic of interest to physical oceanographers for several decades. This area has recently been reviewed by Hogg (1980) and was the topic of a monograph by Kozlov (1983). Taylor columns, semistationary eddies located above seamounts, have been theoretically predicted and experimentally demonstrated for several decades (Taylor 1917; Huppert and Bryan 1976); they have been observed over some seamounts (Darnitsky 1980b; Owens and Hogg 1980; Richardson 1980). Taylor columns are likely generated over central N Pacific seamounts, where eddies have been observed (Cheney et al. 1980; Darnitsky 1980a); unfortunately oceanographic surveys generally have station patterns inappropriate to detect these open-ocean small-scale or mesoscale phenomena (Roden 1986). Still, past theoretical and observational studies on the physics of topographic effects are available to serve as a background for biological studies.

Many studies have suggested that ecosystems at banks or seamounts are highly productive (Uda and Ishino 1958; Fedosova 1974; Bezrukov and Natarov 1976; Zaika and Kovalev 1984; Tseitlin 1985). The ideas which explain such high productivity are typically based upon either local enhancement and subsequent retention of productivity or advection and concentration of food produced elsewhere. Some support exists for each of these hypotheses. Differences often exist between the pelagic ecosystems of waters above seamounts and adjacent, oceanic waters, including plankton biomass (Bezrukov and Natarov 1976), ichthyoplankton (Nellen 1973), and chlorophyll (Genin and Boehlert 1985). In the case of advected productivity, however, seamount populations may not be limited by local production, but rather by physical aggregation mechanisms (Isaacs and Schwartzlose 1965; Darnitsky et al. 1984), which have been

**Fig 1** The S Emperor - N Hawaiian Ridge seamounts. Current flow in this region is dominated by easterly flow from the Kuroshio N of the subtropical front, but this front can vary seasonally (and interannually) between lat. 28° and 32°N (Roden 1970); S of the front, westerly flow may be observed.


EMPEROR SEAMOUNT CHAIN
Koko Seamount
Kimmei Seamount
Yuryaku Seamount
MILWAUKEE SEAMOUNT GROUP
Kammu Seamount
Daikakuji Seamount
Colahan Seamount
C-H Seamount
N.W. Hancock Seamount
HANCOCK SEAMOUNTS
S.E. Hancock Seamount
HAWAIIAN RIDGE
Seamount No. 10
Seamount No. 11
Wenthworth Seamount
Ladd Seamount
KURE I.
MIDWAY IS.
Nero Seamount
PEARL & HERMES REEF
Seamount No. 9
Seamount No 8
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shown to exist in a variety of situations (Alldredge and Hamner 1980; Olson and Backus 1985). In the present paper I describe the effects of an open-ocean seamount on the distribution and abundance of planktonic and micronektonic organisms.

## Materials and Methods

Sampling was conducted at the Hancock Seamounts in the central N Pacific, some 180 nmi NW of Kure Atoll, the nearest emergent land (Fig 1). Each of the two seamounts on this large bank (Southeast Hancock, lat. 29°48'N, long. 178°05'E; Northwest Hancock, lat. 30°17'N, long. 178°44'E) rise to within approximately 265 m of the surface from a background bottom depth of nearly 5 km. Samples described in this study were taken during two cruises of the NOAA ship *Townsend Cromwell* to these seamounts in July-August 1984 and January-February 1985.

A variety of physical measurements were made during these cruises (Brainard and Wittman 1985), but for the purposes of this paper, only thermal structure and summer surface currents will be described. Temperature profiles were taken with expendable bathythermographs (XBT, T-4, Sippican Corp.), which record to 450 m, well below the depth of the seamount summit. Surface bucket thermometer observations were made to check on the XBT readings at the surface. On the summer 1984 cruise, surface currents were estimated with 13 radio-tracked Lagrangian drifters drogued at a depth of 10 m.

Biological sampling was conducted with several gear types. The behavior of seamount-associated scattering layers was observed with a 38 kHz Simrad echo sounder and a Raytheon-JRC chromoscope configured as a slave indicator for the Simrad. Micronekton samples from the scattering layers were taken with a 1.8 m Isaacs-Kidd midwater trawl (IKMT) fitted with a calibrated General Oceanics flowmeter to estimate volume filtered. Appropriate mesh sizes were used to minimize extrusion of the taxa considered in this report. Tows with the IKMT were taken above both SE and NW Hancock Seamounts; comparison tows were taken at reference stations ranging from 2 to 20 km from the summit to determine the composition and abundance of micronekton in oceanic waters. All IKMT hauls were taken at night. Hauls over the seamount were typically targeted to fish within scattering layers; hauls away from the seamount targeted scattering layers if they were evident or were fished at the same depths as those over the seamount if they were not.

Ichthyoplankton samples were taken with a three-net Tucker trawl with a messenger-actuated closing device in the manner described by Boehlert et al. (1985). All nets taking samples were equipped with calibrated flowmeters. Duplicate

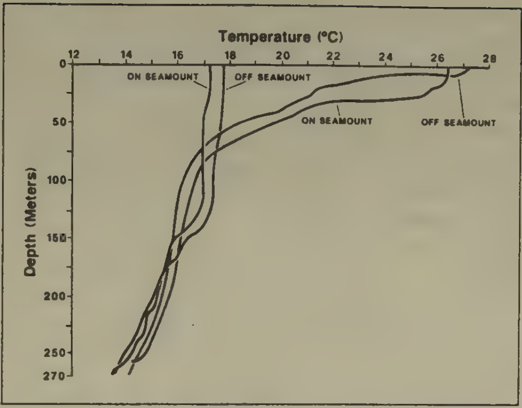
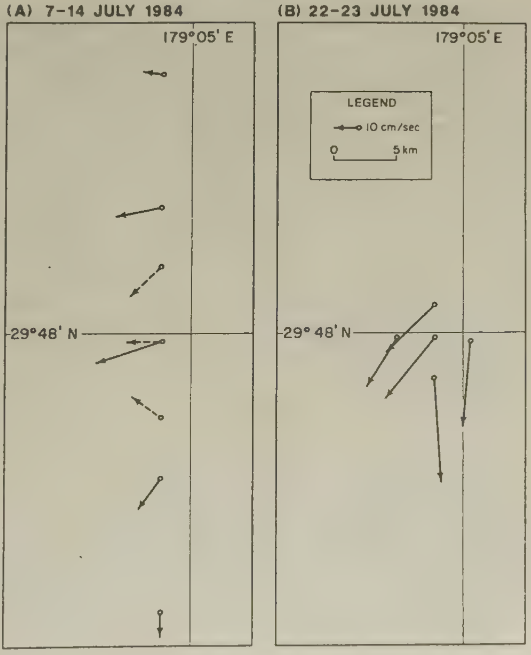


**Fig 2** Temperature-depth profiles taken at SW Hancock Seamount in summer 1984 (warm surface temperatures) and winter 1985. The "on seamount" profiles were taken near the center of the seamount summit, the "off seamount" profiles at a reference station some 20 km distant from the summit.

**Fig 3** Surface current patterns at SE Hancock Seamount for two periods during summer 1984. Magnitude of current speed is indicated by the length of the arrows. These data are based upon radio-tracked Lagrangian drifters drogued at 10 m for periods ranging from 10 to 41 hours. Although the drift trajectories were calculated over several intervening periods, the direction shown is based upon the starting and ending positions. The location of the seamount summit is indicated by the intersection of the two lines.


(A) 7–14 JULY 1984

(B) 22–23 JULY 1984

samples were taken as stepped oblique tows within discrete depth zones of 0-25, 25-50, 50-100, and 100-200 m both day and night. Seamount hauls were made over the summit of SE Hancock Seamount, while the reference station was 20 km west of the seamount summit. All biological samples were immediately preserved in 10% Formalin in seawater buffered with sodium borate. In the laboratory, specimens were sorted from the entire volume of each sample.

## Results

The physical environment differed between summer and winter at these seamounts, as has been described generally by Fedosova (1974) and Darnitsky et al. (1984). Surface temperatures were generally between 26° and 28°C in the summer and 17° and 18°C in winter (Fig 2). A strong thermocline was present near 70 m in summer but the surface waters were well mixed to 120 m or more in winter. A comparison of the thermal structure above the seamounts and at reference stations shows differences between summer and winter. Although these XBT casts were not taken synoptically, they are representative of the temperature patterns observed in many XBT casts. In summer, the temperature above the seamount was typically warmer than at corresponding depths at the reference station; the reverse was true in winter (Fig 2).

Current patterns in summer 1984 were estimated from 13 drogues released on three different dates. Surface currents ranged from 9 to 42 cm/sec and were westward in the first set but directed more southward in the second set (Fig 3).

Hydroacoustic observations on both summer and winter cruises were generally taken from early evening to morning to observe the behavior of seamount-associated scattering layers. Scattering layers were better developed during the summer cruise and were most consistent from night to night as compared to winter; they will thus be discussed in most detail here. During daylight hours, scatterers were distinct on the flanks of the SE Hancock Seamount at depths of approximately 400 m. As dusk approached, the scatterers began streaming vertically upward to depths near 50 m (Fig 4A). This was followed by consolidation of the shallow layers, a slight sinking of the top layer, and expansion downwards until the scattering layer extended from the summit of the seamount upwards to approximately 100 m depth (Fig 4B). The layer remained relatively stationary and coherent throughout the night; as light intensity increased the following morning, some scatterers dispersed upwards, reaching near-surface waters (Fig 4C). As the sun came over the horizon, these shallow layers consolidated and moved rapidly downward. Some scatterers remained in the water column above the seamount flanks later in the morning, present at depths as shallow as 170 m (Fig 4D). No deep scattering layers in surrounding

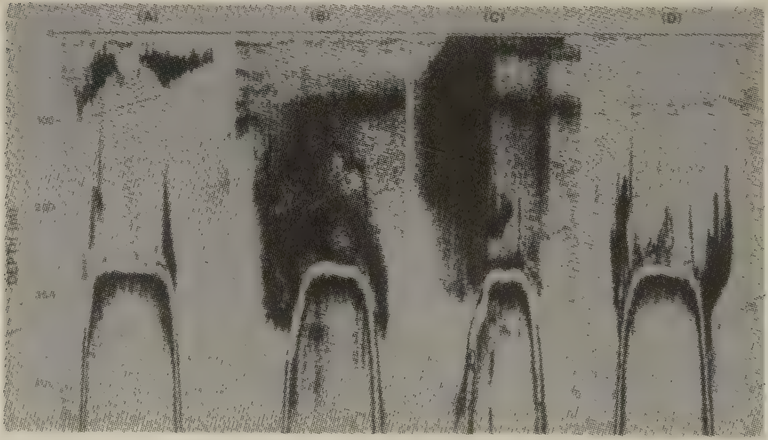


Fig 4
Time series of acoustic transects over SE Hancock Seamount on 17-18 July 1984 showing behavior of the scatterers. Each transect, from W to E (left to right) near the central axis of the seamount, took approximately 25 minutes. The distance across the flat portion of the seamount is approximately 1.8 km.

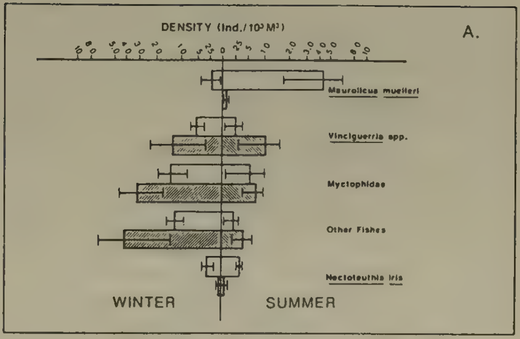
A. 1931 h. Note the scattering layers rising off the seamount flanks to a depth of 40-60 m; net samples show these early layers to be predominantly "Maurolicus muelleri". Sunset was at 1970 h.
B. The layer has developed around the seamount extending from the flanks upwards to near 100 m; it developed this configuration at approximately 2130 h and remained similar throughout the night. This transect was at 0330 h.
C. 0430 h. As light intensity increased, the layer dispersed and moved rapidly upward. As the sun came over the horizon at 0515 h, however, the layer consolidated and moved rapidly downward.
D. 0630 h. The scattering layers remained high in the water column above the flanks later into the morning. These scattering targets may have been larger fishes or squids not sampled by our midwater trawl.

oceanic waters displayed either such high density or this type of behavior, suggesting that organisms specific to the region of the seamount were responsible for the acoustic traces.

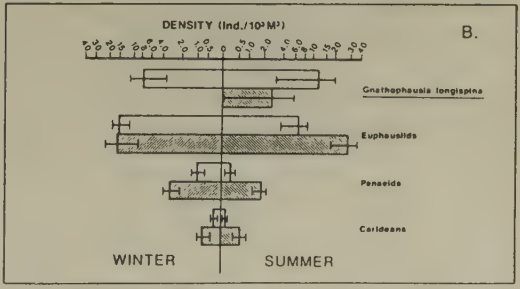
Micronekton samples from the IKMT were generally different between waters above the seamount and at the reference stations. In the summer samples (Fig 5) the sternoptychid fish, *Maurolicus muelleri*, and the lophogastrid mysid, *Gnathophausia longispina*, dominated the catch over the seamounts. A third species, the sepiolid squid, *Nectoteuthis (Iridioteuthis) iris*, was characteristic of the deeper portions of the seamount scattering layer. Early evening IKMT hauls through the scattering layer in shallow water (Fig 4A) were typically dominated by *M. muelleri* with very few crustaceans; later samples included larger catches of *G. longispina* and euphausiids. Since the net was open at all times, samples taken above the seamount were only in the scattering layers for about 50% of the sampling time; thus the estimates of the seamount-associated micronekton are minimum values.

Micronekton samples taken at the reference stations differed in both abundance and composition as compared to seamount samples. Oceanic taxa were generally more abundant, suggesting that the oceanic ecosystem is affected by the seamount or its biota. The three seamount taxa were either absent or in low abundance. The photichthyid fish *Vinciguerria attenuata* and *V. nimbaria* were more abundant in waters away from the seamount, while densities of myctophids and all other fishes combined were not significantly different (Fig 5A). All oceanic crustacean groups, however, were significantly more abundant in tows away from the seamount (Fig 5B). In winter months, most of the same taxa were present, with similar relationships between on- and off-seamount hauls; the exception to this statement is the very low abundance of *M. muelleri* over the seamounts (Fig 5A) and higher relative densities of euphausiids above the seamount (Fig 5B).

Ichthyoplankton densities from the summer cruise taken in daytime showed no difference between samples over the seamount and those at the reference station with the exception of the 50-100 m stratum (Fig 6A). At night, however, the densities at the reference station were significantly increased as compared to daytime values, but there was no corresponding density increase in the samples taken over the seamount. Thus at all depths, there were significantly fewer larvae present over the seamount than at the reference station. In these samples, shallow layers were dominated by the gonostomatid *Cyclothone* spp. and deeper ones (>50 m) by the myctophid *Diogenichthys atlanticus*. These relatively passive components of the plankton reflect the same pattern as the migrating micronekton (Figs 5A,B) during summer months. Samples taken on the winter cruise showed a different pattern from that in the summer (Fig 6B); ichthyoplankton densities over the seamount were much greater than at the reference station, and the pattern held for both night and day. While there were fewer *Cyclothone* in the samples, they were nonetheless dominated by midwater fish taxa as opposed to seamount-associated fishes.



Squids–Fishes



Crustacea

Fig 5 Densities of selected micronekton taxa captured in the Isaacs-Kidd midwater trawl samples.
A. Fishes and squid. - B. Crustacea.
In each panel, data from the summer 1984 cruise are on the right, winter 1985 on the left. In the summer cruise, data are from 12 hauls over the summit and 6 hauls at reference stations; the corresponding numbers for the winter cruise are 12 and 10, respectively. Two values are represented for each taxon; the upper (solid) bar indicates mean density (± 2 S.E.) from the tows over the seamount while the lower (cross-hatched) bar indicates mean densities in off-seamount tows.

## Discussion

Seamounts and other complex topography may be the sites of aggregations of many animals, including tunas (Yasui 1986), marine mammals (Hiu 1985), and other organisms which apparently feed on prey aggregations found at physical discontinuities (Uda and Ishino 1958). There may also be relative enrichment of the benthos in such locations (Genin et al. 1986). Studies of sonic scat-

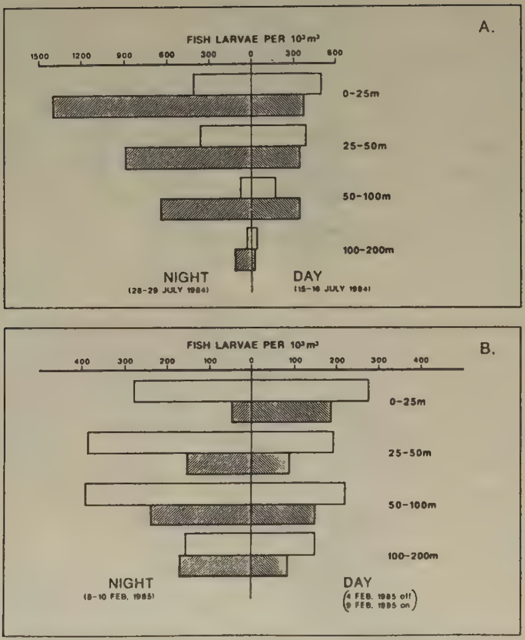


**Fig 6** Ichthyoplankton densities near SE Hancock Seamount taken in Tucker trawl samples.
A. Summer 1984. - B. Winter 1985.
Daytime densities are on the right, nighttime on the left, with each value the mean of duplicate samples. Densities above the seamount are represented by the upper (solid) bar, densities at the reference station by the lower (cross-hatched) bar.

tering layers in wide ocean areas have demonstrated increased plankton or micronekton biomass near banks and islands (Hargreaves 1975); similarly, plankton biomass may increase around islands (Jones 1962). Few studies, however, have demonstrated the high densities of selected micronekton taxa observed over Hancock Seamount (Fig 5), suggesting that the presence of the seamount in some manner induces aggregation of these animals. Abundance of the three organisms we designate as seamount-associated micronekton *(M. muelleri, G. longispina,* and *N. iris)*, is unexpected in mid-ocean regions. *Maurolicus muelleri*, also known as the lightfish, is a cosmopolitan species often found in very high abundance but generally near continental shelf-slope break regions (Robertson 1976; Okiyama 1981); despite several midwater trawl surveys, it is not known from oceanic regions (Barnett 1984). Densities reported in this study are as high as 13.8 per $10^3$ m$^3$ in summer and 1.2 per $10^3$ m$^3$ in winter. *Gnathophausia longispina* is a shallow living member of this mysid genus and the only one which migrates vertically (Clarke 1962); it has been taken in the past only in small numbers but in this study, an average of 105 per positive tow in summer (with a maximum density of 42.7 per $10^3$ m$^3$) and 78 in winter were taken. Finally, *N. iris* is a poorly known species which we have taken in previous bottom trawls on Hancock Seamounts; although present in our midwater trawls, it has been called a predominantly bottom-associated form, similar to other members of the subfamily Heteroteuthinae (Young 1978).

Densities of oceanic taxa of both micronekton (Fig 5) and fish larvae (Fig 6) above the seamount differ from that in adjacent waters, suggesting that they are in some way impacted by the seamount. Similar results with ichthyoplankton have been noted in the past, but the changed densities were typically neritic species (Nellen 1973). This phenomenon was not observed, however, over central N Pacific seamounts (Borets and Sokolovsky 1978) or in the Indian Ocean (Belyanina 1985). The generally lower abundance of oceanic taxa and population maintenance of the seamount-associated taxa can be explained by biological and physical mechanisms and I provide here three hypotheses which, in combination, may help explain the observed phenomena, as follows:

- current-topography interaction forms semistationary eddies or Taylor columns in the region of the seamount;
- the seamount serves to exclude upward vertical migrators from waters above the seamount;
- predation by resident fauna reduces abundance of oceanic species.

Taylor columns could be important both in maintaining planktonic or micronektonic populations and, through upwelling, could increase primary and secondary productivity (Genin and Boehlert 1985). From a theoretical standpoint, Taylor column formation is a function of current strength, seamount morphology, stratification of the water column, and latitude (Huppert 1975). Anticyclonic flow around the seamount should exist, with cold water at its center; warm water cyclonic eddies would remain in the vicinity of the seamount at low current speeds and are shed downstream at higher current speeds (Owens and Hogg 1980). Such a semistationary water column or eddy could maintain the observed community of seamount-associated micronekton. Surface currents over SE Hancock Seamount averaged 22.4 cm/sec (Fig 3) during our summer survey; it is unlikely that the small micronektonic *Gnathophausia* and *Maurolicus* could maintain their horizontal position at distances up to 190 m above seamount in such a current regime, but the scattering layers persisted throughout the night. It is also interesting that after the initial rise to shallower depths (Fig 4A), the top of the scattering layer appears truncated (Fig 4B) near the bottom of the mixed layer (Fig 2), suggesting that a trapped Taylor column (Dooley 1984), not reaching the surface, might be present. Theoretical calculations (Huppert 1975; Huppert and Bryan 1976) based upon the physical characteristics of SE Hancock Seamount and the observed summer current regime would predict the presence of a Taylor column.

The lower abundance of many of the oceanic micronekton in waters above the seamount (Fig 5) may be explained by exclusion of vertical migrators. The relative decrease in density of many of the oceanic crustaceans over the seamount seems to be related to size, which in turn may be related to the magnitude of vertical migration (Roger and Grandperrin 1976). This mechanism would likely interact with any stationary water column, however, since under uniform flow past the seamount, the water column would be completely replaced by advection after two to three hours, resulting in densities which should be similar to those of the reference stations.

The reduction in oceanic taxa, including ichthyoplankton, may also be related to predation. Many of the resident fishes of these seamounts, which may occur in high biomass, feed primarily upon oceanic micronekton and particularly on these larger crustaceans (Fedosova 1976; Humphreys and Tagami 1986). A predation-mediated reduction is also supported by the decreased nighttime densities of larval fishes over the seamount in summer (Fig 6A); these organisms are of the appropriate size spectrum for prey of *M. muelleri* (Hirota and Boehlert 1985), which has a very high biomass during that period (Fig 5). The lack of a difference in summer daytime densities, moreover, is consistent with the absence of *M. muelleri* from the water column during the day (Fig 4). The low abundance of *M. muelleri* in winter months may result in reduced predation on ichthyoplankton but cannot explain the higher abundance above the seamount (Fig 6B).

The observed patterns of micronekton and ichthyoplankton distributions may be based upon a combination of the hypotheses described above. The maintenance of high densities of seamount-associated micronekton over seamounts, however, must require a large forage base. In turn, these micronektonic species probably served as a part of the forage base for higher trophic levels. An important fishery existed on Hancock and several of the S Emperor Seamounts; between 1967 and 1975, nearly one million metric tons of pelagic armorhead, *Pseudopentaceros wheeleri*, were taken from these seamounts by Soviet and Japanese trawlers, and standing stocks of nearly 400,000 metric tons were estimated (Borets 1975; Sasaki 1986). Some of the same physical mechanisms which alter the patterns of distribution and abundance of the taxa as described in this paper may be invoked to explain the availability of the energy necessary to maintain high densities of fish. First, convergent flow resulting in accumulation of the background oceanic plankton and micronekton may provide prey (Isaacs and Schwartzlose 1965; Darnitsky et al. 1984; Tseitlin 1985). Secondly, upwelling associated with flow around topography may increase nutrients and biological productivity in surface waters (Uda and Ishino 1958; Genin and Boehlert 1985); in this case, however, there must be some mechanism by which this productivity is retained in the region of the seamount. A Taylor column or other stationary water mass could retain this productivity, but the residence times of such features are unknown.

It is clear from these results that seamounts induce biological variability in mid-ocean pelagic ecosystems. Above this seamount I observed depletion of some organisms and abundance of others (Fig 4, 5, 6). Interacting with oceanic currents, seamounts apparently generate and shed mesoscale eddies which are detectable downstream (Royer 1978). Eddies may maintain their integrity with respect to physical and biological characteristics for long periods (Ortner et al. 1978; Owen 1981; Olson and Backus 1985; Wiebe et al. 1985). Thus eggs, larvae, and even adults of seamount-associated species may occur in isolated eddies distant from the seamounts, which could similarly be depleted in oceanic species. Since current speed plays such an important role in the physical dynamics of these systems (Huppert and Bryan 1976; Kozlov 1983), interannual variability in the magnitude and direction of ocean currents can have strong effects on the productivity of these ecosystems. Interannual variability in the latitudinal position of the subtropical front, which will exert strong effects in the region of the Hancock Seamounts (Fig 1) is well known (Roden 1970). Similarly, interannual variability in eddy production has been observed in the Kuroshio system (Mizuno and White 1983). Further understanding of the interaction of currents with mid-ocean seamounts will be necessary to understand the dynamics of these unique ecosystems.

## References

Alldredge, A.L.; Hamner, W.M.: Recurring aggregations of zooplankton by a tidal current. Est. Coastal Mar. Sci. 10, 31-37 (1980)

Barnett, M.A.: Mesopelagic fish zoogeography in the central tropical and subtropical Pacific Ocean: species composition and structure at representative locations in three ecosystems. Mar. Biol. 82, 199-208 (1984)

Belyanina, T.N.: Preliminary data on ichthyoplankton of seamount regions of the northwestern Indian Ocean. Okeanologiya, SSSR. 25,6, 1013-1016 (1985)

Bezrukov, Y.F.; Natarov, V.V.: Formation of abiotic conditions over the submarine eminences of some regions of the Pacific Ocean. Izv. Pac. Sci. Res. Inst. Fish. Oceanogr. (TINRO) 100, 93-99. (Translation by W.G. Van Campen, 1983, available at NMFS Honolulu Laboratory) (1976)

Boehlert, G.W.: Productivity and population maintenance of seamount resources and future research directions. In: Uchida, R.N.; Hayasi, S.; Boehlert, G.W. (eds.), Environment and resources of seamounts in the North Pacific. US Dep. Commer., NOAA Tech. Rep. NMFS 43, 1986.

Boehlert, G.W.; Gadomski, D.M.; Mundy, B.C.: Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull., US 83, 611-621 (1985)

Borets, L.A.: Some results of studies on the biology of the boarfish ("Pentaceros richardsoni" Smith). Investigations of the Biology of Fishes and Fishery Oceanography, No. 6, TINRO, Vladivostock 1975.

Borets, L.A.; Sokolovsky, A.S.: Species composition of ichthyoplankton of the Hawaiian submarine ridge and Emperor Seamounts. Izv. Pac. Sci. Res. Inst. Fish. Oceanogr. (TINRO) 102, 43-50 (1978)

Brainard, R.E.; Wittman, P.: Aspects of the thermohaline structure over Southeast Hancock Seamount. EOS, Trans. Am. Geophys. Union 66, 1336 (1985)

Cheney, R.E.; Richardson, P.L.; Nagasaka, K.: Tracking a Kuroshio cold ring with a free-drifting surface buoy. Deep-Sea Res. 27A, 641-654 (1980)

Clarke, W.D.: The genus "Gnathophausia" (Mysidacea, Crustacea), its systematics and distribution in the Pacific Ocean. Ph.D. Dissertation, Univ. Calif., 251 p., 1962.

Darnitsky, V.B.: Baroclinic and barotropic topographic vortices in the ocean. Problems in Oceanography (State Committee of the USSR for Hydrometeorology and Environmental Monitoring) 86, 51-62, 1980a.

Darnitsky, V.B.: On the synoptic variability of the geostrophic circulation in areas of underwater rises in the North Pacific Ocean. Problems in Oceanography (State Committee of the USSR for Hydrometeorology and Environmental Monitoring) 86, 63-70, 1980b.

Darnitsky, V.B.; Boldyrev, B.L.; Volkov, A.F.: Environmental conditions and some ecological characteristics of fishes from the central North Pacific seamounts. In: Proceedings, Conditions of Formation of Commercial Fish Concentrations, Ministry of Fisheries, USSR, All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO) p. 64-77. Moscow 1984.

Dooley, H.D.: Aspects of oceanographic variability of Scottish fishing grounds. Ph.D. Thesis, Univ. Aberdeen, Scotland, 154 p., 1984.

Fedosova, R.A.: Distribution of some copepod species in the vicinity of the underwater Hawaiian Ridge. Oceanology 14, 724-727 (1974)

Fedosova, R.A.: Some data on the feeding of boarfish, "Pentaceros richardsoni" Smith, on the banks of the Hawaiian Ridge. Trudy TINRO 7, 29-36 (1976)

Genin, A.; Boehlert, G.W.: Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. J. Mar. Res. 43, 907-924 (1985)

Genin, A.; Dayton, P.K.; Lonsdale, P.F.; Speiss, F.N.: Corals on seamount peaks: evidence of current acceleration over deep-sea topography. Nature 322, 59-61 (1986)

Hargreaves, P.M.: Some observations on the relative abundance of biological sound scatterers in the northeastern Atlantic Ocean, with particular reference to apparent fish shoals. Mar. Biol. 29, 71-87 (1975)

Hirota, J.; Boehlert, G.W.: Feeding of "Maurolicus muelleri" at Southeast Hancock Seamount and its effects on the zooplankton community. EOS, Trans. Am. Geophys. Union 66, 1336 (Abstr.) (1985)

Hogg, N.G.: Effects of bottom topography on ocean currents. In: GARP Publication Series No. 23, p. 167-205. WMO-ICSU 1980.

Hui, C.A.: Undersea topography and comparative distributions of two pelagic cetaceans. Fish. Bull., US 83, 472-475 (1985)

Humphreys, R.L. Jr.; Tagami, D.T.: Review and current status of research on the biology and ecology of pelagic armorhead. In: Uchida, R.N.; Hayasi, S.; Boehlert, G.W. (eds.), Environment and Resources of Seamounts in the North Pacific. US Dep. Commer., NOAA Tech. Rep. NMFS 43, 1986.

Huppert, H.E.: Some remarks on the initiation of inertial Taylor Columns. J. Fluid Mech. 67, 347-312 (1975)

Huppert, H.E.; Bryan, K.: Topographically generated eddies. Deep-Sea Res. 23, 655-679 (1976)

Hurlburt, H.E.; Thompson, J.D.: Preliminary results from a numerical study of the New England Seamount Chain influence on the Gulf Stream. In: Holloway, G.; West, B.J. (eds.), Predictability of Fluid Motions, p. 489-503. Am. Inst. Physics, New York 1984.

Isaacs, J.D.; Schwartzlose, R.A.: Migrant sound scatterers: Interactions with the sea floor. Science 150, 1810-1813 (1965)

Jones, E.C.: Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Islands, Central Pacific. J. Cons. int. perm. Explor. Mer 27, 223-231 (1962)

Kozlov, V.F.: Models of topographic vortices in the ocean. Pacific Oceanological Institute, Academy of Sciences of the USSR, 199 p. Nauka, Moscow 1983.

Kozlov, V.F.; Darnitsky, V.B.; Ermakov, M.I.: An experiment in modeling topographic vortices over underwater mountains. Problems in Oceanography (State Committee of the USSR for Hydrometeorology and Environmental Monitoring) 96, 3-25, 1982.

Manheim, F.T.: Marine cobalt resources. Science 232, 600-608 (1986)

Mizuno, K.; White, W.B.: Annual and interannual variability in the Kuroshio Current system. J. Phys. Oceanogr. 13, 1847-1867 (1983)

Nellen, W.: Untersuchungen zur Verteilung von Fischlarven und Plankton im Gebiet der Grossen Meteorbank. "Meteor" Forsch.-Ergebnisse 13, 47-69 (1973)

Okiyama, M.: Abundance and distribution of eggs and larvae of a sternoptychid fish, "Maurolicus muelleri", in the Japan Sea, with comments on the strategy for successful larval life. Rapp. P.-V. Reun. Cons. int. Explor. Mer 178, 246-248, 1981.

Olson, D.B.; Backus, R.H.: The concentrating of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. J. Mar. Res. 43, 113-137 (1985)

Ortner, P.B.; Wiebe, P.H.; Haury, L.; Boyd, S.: Variability in zooplankton biomass distribution in the northern Sargasso Sea: The contribution of Gulf Stream cold core rings. Fish. Bull., US 76, 323-334 (1978)

Owen, R.W.: Fronts and eddies in the sea: Mechanisms, interactions, and biological effects. In: Longhurst, A.R. (ed.), Analysis of marine ecosystems, p. 197-233. Acad. Press, New York 1981.

Owens, W.B.; Hogg, N.G.: Oceanic observations of stratified Taylor columns near a bump. Deep-Sea Res. 27A, 1029-1045 (1980)

Richardson, P.L.: Anticyclonic eddies generated near the Corner Rise seamounts. J. Mar. Res. 38, 673-686 (1980)

Robertson, D.A.: Planktonic stages of "Maurolicus muelleri" (Teleostei: Sternoptychidae) in New Zealand waters. N.Z. J. Mar. Freshwater Res. 10, 311-328 (1976)

Roden, G.I.: Aspects of the mid-Pacific transition zone. J. Geophys. Res. 75, 1097-1109 (1970)

Roden, G.I.: Aspects of oceanic flow and thermohaline structure in the vicinity of seamounts. In: Uchida, R.N.; Hayasi, S.; Boehlert, G.W. (eds.), Environment and Resources of Seamounts in the North Pacific. US Dep. Commer., NOAA Tech. Rep. NMFS 43, 1986.

Roden, G.I.; Taft, B.A.; Ebbesmeyer, C.C.: Oceanographic aspects of the Emperor Seamounts region. J. Geophys. Res. 87, 9537-9552 (1982)

Roger, C.; Grandperrin, R.: Pelagic food webs in the tropical Pacific. Limnol. Oceanogr. 21, 731-735 (1976)

Royer, T.C.: Ocean eddies generated by seamounts in the North Pacific. Science 199, 1063-1064 (1978)

Sasaki, T.: Development and present status of Japanese trawl fisheries in the vicinity of seamounts. In: Uchida, R.N.; Hayasi, S.; Boehlert, G.W. (eds.), Environment and Resources of Seamounts in the North Pacific. US Dep. Commer., NOAA Tech. Rep. NMFS 43, 1986.

Taylor, G.I.: Notion of solids in fluids when the flow is not irrotational. Proc. Roy. Soc. A93, 99-113 (1917)

Tseitlin, V.B.: The energetics of the fish population inhabiting the underwater mountain. Okeanologiya 25,2, 308-311 (1985)

Uchida, R.N.; Hayasi, S.; Boehlert, G.W. (eds.): Environment and resources of seamounts in the North Pacific. US Dep. Commer., NOAA Tech. Rep. NMFS 43, 1986.

Uda, M.; Ishino, M.: Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo Univ. Fish. 44, 105-129 (1958)

Vastano, A.C.; Warren. B.A.: Perturbations to the Gulf Stream by Atlantis II Seamount. Deep-Sea Res. 23, 681-694 (1976)

Wiebe, P.H.; Flierl, G.R.; Davis, C.S.; Barber, V.; Boyd, S.H.: Macrozooplankton biomass in Gulf Stream warm-core rings: spatial distribution and temporal changes. J. Geophys. Res. 90, 8885-8902 (1985)

Yasui, M.: Albacore, "Thunnus alalunga", pole and line fishery around the Emperor Seamounts. In: Uchida, R.N.; Hayasi, S.; Boehlert, G.W. (eds.), Environment and Resources of Seamounts in the North Pacific. US Dep. Commer., NOAA Tech. Rep. NMFS 43, 1986.

Young, R.E.: Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish. Bull., US 76, 583-616 (1978)

Zaika, V.E.; Kovalev, A.V.: The study of the ecosystems of submarine mountains. Biol. morya (Vladivost.) 1984,6, 3-8 (1984)

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# FISHING IN THE EXCLUSIVE ECONOMIC ZONE: THE POTENTIAL FOR ISLAND-RELATED RESOURCES

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The series of discussions on fishing in the EEZ which follow will distinguish among several types of resources. They differ in biological make-up, magnitude, and commercial value as one goes from region to region. A basic biological distinction of resources exploited in island areas is that of pelagic versus insular. Pelagic resources occur throughout the EEZ irrespective of water depth, although they are frequently encountered near thermal fronts or other oceanographic features. Insular resources are concentrated in very narrow bands around islands, seamounts, or shallow banks. Unlike pelagic resources, they are typically nonmigratory.

In this paper, I cover island-related resources, which are less controversial than migratory species, but nonetheless quite important locally. I briefly address the types of resources, their relationship to the habitat, their potential magnitude, and finally the importance of managing these insular resources.

## Types of Insular Resources

Insular resources consist of both shallow reef species and deep slope species. Shallow reef resources include reef fishes, crustaceans (lobster, crab, and shrimp), mollusks (octopus, and clams), and echinoderms (Beche-de-Mer). In most islands, the majority of these resources are already exploited and many are important for artisanal and subsistence fishing. There is little potential for fisheries expansion, save the uncertain potential of aquaculture. Therefore, I will concentrate this paper on the slope resources, which hold greater potential in most island areas.

Generally, the slope resources occur in the 20 to 500 fathom depth range and are less well known than reef resources, especially in unpopulated regions. Throughout the Pacific island areas, several ongoing projects are directed at determining the magnitude and potential management regimes for the resources. The types of resources available include precious corals, bottom fishes, and crustaceans.

Precious corals typically occur in deeper waters and are most heavily exploited on banks and seamounts in international waters. Further exploitation potential does exist, as indicated by recent discoveries of new resources. A fisheries management plan has been developed for precious corals in the Hawaiian Archipelago and other waters under the purview of the WESPAC (see Grigg, 1982).

Bottom fish represent a real multispecies fishery in the most tropical regions. Accordingly, the resulting high species diversity is exploited. The techniques for harvesting this resource are labor intensive relative to some of the large scale fisheries in temperate and artic regions and generally involve handlines, longlines, or fish traps. The species involved include several families. The snappers (family Lutjanidea) are commercially important and include onaga, ehu, opakapaka, and several others. Snappers occur in a range of sizes, but are generally of high value. The groupers (family Serranidea) include only the hapuupuu in Hawaii, but have several other representatives in other parts of the Pacific. Other families include the jacks (family Carangidae), emperors (family Lethrinidae), and a suite of less common varieties.

Crustacean fisheries are typically conducted with traps. In tropical island areas, lobster and shrimp have considerable economic potential. In the Hawaiian Archipelago, the lobster fishery captures spiny and slipper lobsters, both now subject to a fishery management plan to regulate the harvest. With the exception of precious corals, deep sea shrimps (Heterocarpus, spp.) are the deepest slope resource taken in the tropical Pacific. The magnitude of the resource is apparently extensive in Hawaii, but there is not a significant fishery at the present time.

In general, the majority of insular stocks are characterized by a low biomass, fairly low turnover rate, and a very limited habitat. Managing the stocks will require managing not only the fishery, but also the habitat. Island types range from volcanic islands to coral atolls, to very large limestone islands. A common feature of most of the islands is the relatively steep profile underwater. An extensive shelf, as occurs on continents, is not present. For this reason, the fisheries are referred to as slope fisheries. As opposed to the resources on continental shelves, which are often quantified per square nautical mile, the resources on steep slopes are generally quantified per linear mile of isobath at a given depth. In the rather rare cases where moderately flat bottom occurs, the productivity may be low. A good example is the Penguin Bank region off the Island of Molokai. Productive fishing occurs only around the margin of the bank where bottom relief is high. Thus, the type of habitat and its interactions with currents play an important role in determining the fisheries' productivity.

## The Magnitude of Insular Resource

The magnitude of insular resources is not great. As examples, I will provide data from two large, extensive, archipelagoes. First, the Hawaiian Archipelago consists of the main islands with a long history of fisheries exploitation and the Northwestern Hawaiian Islands with a much shorter period of exploitation. The latter area was the subject of a multiagency program evaluating the resources, and the results have been described in a fishery resource atlas (Uchida and Uchiyama, 1986). Although the EEZ of the Hawaiian Archipelago is quite extensive, the realized and potential yields of the current insular fisheries are surprisingly small. Bottom fish are presently harvested at an annual rate of some 780 metric tons (t) worth about $4.5 million. The lobster catch in the past few years has approached 1,000 t and a value of $6 million. The maximum sustainable yield of this resource over the long-term will probably be somewhat lower than the current yield. Another major insular resource is the deep-sea shrimp which had an annual yield of 160 t in 1984 before ending. Assessment research conducted at the Southwest Fisheries Center Honolulu Laboratory of the NMFS suggests that the resource could annually support a fishery on the order of 300 to 500 t, worth an estimated $3-4 million. This is a trap fishery in deep water, and the fishing technology is not simple. Cessation of the fishery was related to difficulty in harvesting the shrimp, but it is probable that the fishery will develop anew.

The second example is the Mariana Archipelago. rom 1982 to 1985, the Honolulu Laboratory conducted the Resource Assessment Investigation of the Marina Archipelago program (RAIOMA). The goals of this several year field study were assess and map the deep slope resources of this island group. Here, as opposed to the Hawaiian Archipelago, the lobster potential was very low, and the emphasis was instead on bottom fish and deep-sea shrimp. The magnitude of the resources was significantly less, with an estimated annual yield of 109 t of bottom fish and 30-60 t of deep-sea shrimp. The resources are distributed throughout the archipelago. The potential annual yield of bottom fish ranges from <1 to >5 t at different islands or banks. Obviously, the appropriate fisheries here would be small-scale, continuous operations, as opposed to large scale fisheries able to harvest large amounts of the resource at any one time. The RAIOMA program is described further in Polovina et al (1985).

## New Fisheries Resources

A valid question about insular resources of the Pacific Basin concerns the potential discovery of new resources. The deep water nature of the resources such as precious corals and deep-sea shrimps makes them likely to occur in areas not yet surveyed. For example, large discoveries of precious coral beds occur from time to time, as recently happened around Palmyra Atoll. There may also be unanticipated resources. An example of this type is provided by the discovery of seamount resources in the central North Pacific, of which only some 10% occurred within the EEZ waters, and the remainder in international waters. In the southern Emperor Seamount chain and the northern Hawaiian Ridge, several seamount summits rise to within a few hundred meters of the ocean surface. Similar to islands, the habitat that could support fisheries is very limited, and seamounts were thus ignored as sites for fisheries development. However, in 1968, a Soviet trawler discovered dense concentrations of a fish called pelagic armorhead.

Over the next ten years, Soviet and Japanese fishermen took a total catch of approximately 1 million metric tons of this species. Catch rates were as high as 90 t per hour on the Southeast Hancock Seamount, which occurs within the U.S. EEZ; extreme declines in the resource followed this rapid exploitation, until little exploitable biomass remains. The seamounts in the EEZ are presently closed to foreign fishing under the Bottom Fish and Seamount Groundfish Fisheries Management Plan, and research is under way to monitor the recovery of the stock. It has been estimated that the fishery could maintain an annual yield on the order of 50,000 to 80,000 t, which is quite significant relative to the insular resources described earlier in the paper. At the peak of this fishery, a large factory trawler could capture from a single seamount in the EEZ the amount of bottom fish that the entire Hawaiian Archipelago might support over an entire year (Uchida et al. 1986).

In this short paper, I have tried to point out the relatively delicate nature of the island-related fisheries resources in the Pacific Basin. It is critical that managers, politicians, and potential fisheries developers understand the limits of the resources. Resource managers also must have a basic understanding of the biology and exploitation potential for the resources. As opposed to the large scale fisheries of the temperate areas, where catches may be in the thousands of metric tons, these tropical island resources may support fisheries on the order of tens or hundreds of metric tons per year. It is most important to assess these resources in advance of initiating fisheries, even if done in only a cursory fashion. This can have a number of benefits, particularly avoiding the depletion of the resource and over-capitalization by an island nation that cannot afford the investment.

Despite their limited nature, insular resources of the deep slope still play an important role in the Pacific island region. First, such resources are an important source of protein in island areas and may serve to supplement the over fished inshore reef fisheries. Second, the deep slope resources typically have a fairly high market value. At the Honolulu fish auction, one sees bottom fish shipped by air from other islands, so the potential for export markets for foreign exchange does exist. It should be kept in mind, however, that although renewable, these resource can be depleted rapidly.

## REFERENCES

Grigg, R.W., 1982, "Precious coral in the Pacific; economics and development potential." Infofish Marketing dig 2: 8-11.

Polovina, J.J., R.B. Moffitt, S. Ralston, P.M. Shiota, and H.A. Williams, 1985, "Fisheries resource assessment of the Marina Archipelago 1982-1985." Mar. Fish. Rev. 47 (4): 19-25.

Uchida, R.N., S. Hayasi, and G.W. Boehlert (editors), 1986, Environment and resources of seamounts in the North Pacific. U.S. Dept. Commerce, NOAA Tech. Rep. NMFS 43, 105p.

Uchida, R.N., and J.N. Uchiyama (editors), 1986, *Fishery atlas of the Northwestern Hawaiian Islands.*. U.S. Dept. Commerce, NOAA Tech Rep. NMFS 38, 142p.

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Eos, Vol. 69, No. 49, December 6, 1988

## Information Report

# Seamount Acoustic Scattering

## Nocturnal Emissions or Organismal Activities?

PAGES 1619, 1628

The cover of the March 1 issue of *Eos* showed a time series of acoustic scattering above Southeast Hancock Seamount (29°48′N, 178°05′E) on July 17–18, 1984. In a comment on that cover Martin Hovland (*Eos*, August 2, p. 760) argued that gas or "other far reaching causes" may be involved in the observed acoustic signals. He favors a hypothesis that acoustic scattering observed above a seeping pockmark in the North Sea is a combination of bubbles, stable microbubbles, and pelagic organisms and infers that this may be a more general phenomenon and indeed plays a role in the attraction of organisms to seamounts.

Relevant to this issue is our fieldwork conducted and continuing over Southeast Hancock Seamount. Net samples clearly demonstrate that the scattering layers are composed of higher densities of micronektonic organisms, some of which are unique to the seamount ecosystem as opposed to surrounding oceanic waters; the latter species include the sternoptychid fish *Maurolicus muelleri* and the lophogastrid mysid *Gnathophausia longispina* [*Boehlert and Seki*, 1984; *Boehlert*, 1988].

These animals do migrate vertically on a diurnal basis, as do many other oceanic organisms; the form of the acoustically detected mass varies from night to night and is dependent upon current patterns (*C. Wilson*, Honolulu Laboratory, Hawaii, unpublished data). The vertical component of the scattering layers evident in the first and fourth panels of the *Eos* cover are temporary situations based upon vertical movements; the organisms cannot undergo "more horizontal spreading" at a different vertical layer without first getting there through vertical movements. In fact, our net sampling on the nights when the acoustic transects were taken suggests that the animals in the first panel are almost exclusively *M. muelleri*, whereas later migrators include several species of crustaceans. As shown in the second panel, the upper portion of the layer is deeper in the water column, indicating the layer has settled from its initial upward movement. The third panel shows scatterers before dawn extending close to the surface, and the fourth, rapid movement downward. The behavior of the layers is indicative of a biological rather than a gaseous origin.

While our net samples are unable to detect bubbles or stable microbubbles, I believe that the evidence is largely against their existence. Southeast Hancock Seamount is about 30 million years old [*Grigg*, 1988], and no volcanic or hydrothermal activity is evident there or on surrounding seamounts. As is characteristic of relatively shallow seamounts, sediment cover is lacking. Conditions supporting the formation of seeps or bubbles are thus not evident. If gaseous emissions exist, however, one might ask why they would only be nocturnal. One could conceive of a diel periodicity, but the movements of these layers correspond to changing isolumes, and thus, diel periodicity changes seasonally with day length, as does vertical migration in the open ocean [*Boden and Kampa*, 1967]. Moreover, unless the bubbles or stable microbubbles are photoreactive, they would neither disappear nor descend with the rising sun (fourth panel of *Eos* cover and the left panel of Figure 1). Our observations also suggest that continued acoustic scattering occurs off the flanks of the seamount in early morning (right panel of Figure 1).

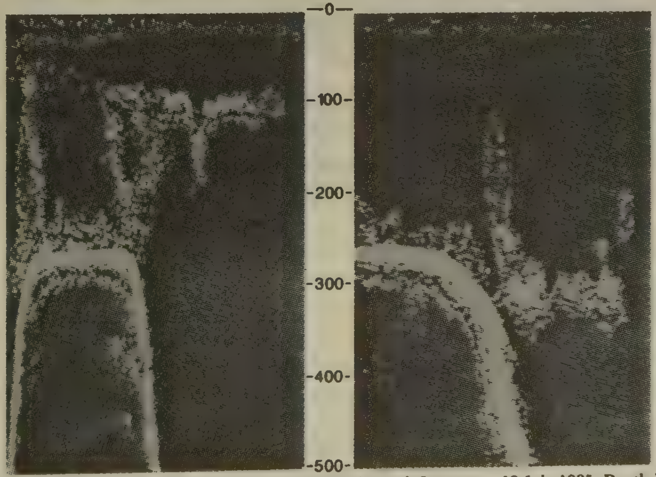

Fig. 1. Acoustic scattering around Southeast Hancock Seamount, 13 July 1985. Depth is in meters. The record is from a 38 kHz Simrad EQ-38 depth sounder photographed from a JRC Chromoscope. The left panel was taken at 0514 as the layer consolidated near 100 m and began its descent. The right panel, at 0654, shows scatterers off the flank of the seamount, well after sunrise. (Reference to the trade name Simrad does not imply endorsement by the National Marine Fisheries Service, NOAA.)

There is no doubt that acoustic scattering increases in association with emergent land and seamounts. *Hargreaves* [1975] conducted acoustic surveys throughout the Atlantic and observed higher levels near seamounts and islands. The well-known island mass effect, which suggests increased primary productivity around islands, may only occur around high islands [*Dandonneau and Charpy*, 1985]. Increased productivity of atolls has been hypothesized to occur through upward percolation of nutrients in limestone (analogous to seeps); this has been termed endo-upwelling by *Rougerie and Wauthy* [1986]. Acoustic evidence of increased biomass near isolated, oceanic seamounts abounds and has been observed at Southeast and Northwest Hancock Seamounts [*Boehlert and Seki*, 1984; *Boehlert*, 1988], Milwaukee Bank in the Emperor Seamounts, Fieberling Seamount off California [*Kozlov et al.*, 1982], and above several seamounts in the South Atlantic [*Kalinowski and Linkowski*, 1983]. All exhibit the pattern of enhanced scattering at night and vertical movements. Seamounts or banks closer to continental shelves do not necessarily show this pattern; *Genin et al.* [1988] demonstrate that resident predators actually deplete oceanic scattering layers above Nidever Bank off the California coast. A similar process probably occurs over oceanic seamounts for certain species [*Borets and Darnitsky*, 1983].

The increased abundance of pelagic organisms near seamounts may be due to several factors, but seepage of gas or liquids is a new idea. At Minami-Kasuga Seamount in the northern Mariana arc, active hydrothermal fields are characterized by abundant benthic macrofauna [*Vonderhaar et al.*, 1987], but earlier studies there showed that planktonic processes, including zooplankton abundance patterns, were a function of hydrographic conditions [*Genin and Boehlert*, 1985].

Current hypotheses on aggregation of pelagic organisms at seamounts have dealt with either enhanced in situ production or mechanisms of aggregation. Although nutrients [*Darnitsky et al.*, 1984] and chlorophyll [*Genin and Boehlert*, 1985] may be enhanced over seamounts through upwelling and retention, the time necessary to transfer any enhanced productivity to higher trophic levels may be longer than the residence time of topographically generated eddies akin to Taylor columns. Thus, other arguments suggest that advected energy (principally zooplanktonic and micronektonic prey organisms) is responsible for higher biomass over seamounts [see review in *Boehlert and Genin*, 1987]. There is little doubt that topographic effects of ocean currents have biological implications [*Wolanski and Hamner*, 1988]; aggregation of pelagic organisms is but one facet.

To conclude, the possibility of seeps and bubbles cannot be completely discounted in explaining increased acoustic scattering over and around seamounts. Further research will be necessary to investigate their effects on plankton and micronekton communities, but a variety of evidence (including that presented above) suggests that they are not the causative agent in the majority of seamount situations studied to date.

## References

Boden, B. P., and E. M. Kampa, The influence of natural light on the vertical migrations of an animal community in the sea, *Symp. Zool. Soc. London*, *19*, 15, 1967.

Boehlert, G. W., Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems, *GeoJournal*, *16*, 45, 1988.

Boehlert, G. W., and A. Genin, A review of the effects of seamounts on biological processes, in *Seamounts, Islands, and Atolls*, *Geophys. Monogr.*, vol. 43, edited by B. H. Keating, P. Fryer, R. Batiza, and G. W. Boehlert, pp. 319–334, AGU, Washington, D.C., 1987.

Boehlert, G. W., and M. P. Seki, Enhanced micronekton abundance over mid-Pacific seamounts (abstract), *Eos*, *65*, 928, 1984.

Borets, L. A., and V. B. Darnitsky, Influence of hydrodynamic processes on the fish productivity of the thalassobathyal; the example of the Hawaiian submarine ridge, *Izv. Pac. Ocean Sci. Res. Inst. Fish. Ocean (TINRO) Vladivostok*, *107*, 47, 1983 (English translation available as Translation No. 124, by W. G. Van Campen, 1988, 11 p., Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822–2396).

Dandonneau, Y., and L. Charpy, An empirical approach to the island mass effect in the south tropical Pacific based on sea surface chlorophyll concentrations, *Deep Sea Res.*, *32*, 707, 1985.

Darnitsky, V. B., N. I. Zigel'man, and S. A. Shakhunova, Variability of the levels of nutrient content in the boundary layer of the Wanganella Bank, *Problems of the Oceanography of the Pacific Ocean and Far Eastern Seas, Gidrometeoizdat, Leningrad*, *111*, 107, 1984 (English translation available as Translation No. 123, by W. G. Van Campen, 1987, 9 p., Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822–2396).

Genin, A., and G. W. Boehlert, Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment, *J. Mar. Res.*, *43*, 907, 1985.

Genin, A., L. Haury, and P. Greenblatt, Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness, *Deep Sea Res.*, *35*, 151, 1988.

Grigg, R. W., Paleoceanography of coral reefs in the Hawaiian-Emperor chain, *Science*, *240*, 1737, 1988.

Hargreaves, P. M., Some observations on the relative abundance of biological sound scatterers in the North- eastern Atlantic Ocean, with particular reference to apparent fish shoals, *Mar. Biol. (Berl.)*, *29*, 71, 1975.

Kalinowski, J., and T. B. Linkowski, Hydroacoustic observations on *Maurolicus muelleri* (Sternoptychidae) over R.S.A. and Discovery Seamounts (South Atlantic), *ICES-CM-1983/H:16*, 1983.

Kozlov, V. F., V. B. Darnitsky, and M. I. Ermakov, An experiment in mathematical modeling of topographic vortices over seamounts, *Problems in Oceanography (State Committee of the USSR for Hydrometeorology and Environmental Monitoring), Leningrad*, *96*, 3, 1982 (English translation from Russian available as Translation No. 119, by W. G. Van Campen, 1987, 25 p., Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822–2396).

Rougerie, F. and B. Wauthy, Atoll-oasis functioning and the endo-upwelling concept, *Ocean. Acta.*, *9*, 133, 1986.

Vonderhaar, D. L., G. M. McMurtry, P. Fryer, and A. Malahoff, Geochemistry of hydrothermal deposits from active submarine volcanoes in the Mariana arc, *Eos*, *68*, 1533, 1987.

Wolanski, E., and W. M. Hamner, Topographically controlled fronts in the ocean and their biological influence, *Science*, *241*, 177, 1988.

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# Roles of Behavioral and Physical Factors in Larval and Juvenile Fish Recruitment to Estuarine Nursery Areas

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*Abstract.*—Recruitment to and maintenance in estuaries are important parts of the early life history of many fish species. Field studies have documented patterns of estuarine recruitment for several species; although some studies have postulated passive mechanisms for recruitment, the majority suggest specific behavior patterns that clearly correlate with physical factors or other stimuli. We consider recruitment to the estuary of species spawned offshore as a two-stage process dependent first upon factors in the offshore planktonic environment and second upon estuarine factors related to tidal flux. Rather than a simple stimulus–response mechanism related to a single physical factor, we suggest that the suite of factors associated with tidal flux at particular locations may act as the zeitgeber for an endogenous rhythm with a tidal periodicity. In this manner, an animal may use tidal-stream transport both for movement into the estuary and for maintenance within the estuary. Further work in the laboratory is necessary to elucidate these behaviors in fishes, particularly those related to endogenous rhythms and the stimuli that serve as zeitgebers.

Use of estuarine nursery areas is an important phase of the life history of many marine organisms, including many commercially valuable shrimps and fishes (McHugh 1967; Staples 1980; Haedrich 1983). The net seaward movement of estuarine waters, combined with tidal flux, causes problems for taxa using estuaries; these problems are generally related to either export from or recruitment to the estuary. Different strategies of estuarine use are apparent among taxa. Several species are resident in estuaries throughout their life histories. Their primary recruitment problem is to prevent the export of early life history stages from the estuary (Johnson and Gonor 1982), and they often solve this by producing large, demersal eggs (Hempel 1979) and having brief larval stages. Species that visit periodically as adults for feeding or spawning face the problem of locating the estuary; if they spawn there, their larvae face the same export problems as the residents. The interactions between hydrographic features of an estuary and population maintenance have traditionally fascinated biologists. Early interest centered upon the ability of planktonic organisms, including larvae, to remain in estuarine systems despite tidal flushing (Rogers 1940; Carriker 1951; Bousfield 1955). Early hypotheses explaining retention in estuaries generally invoked the use by organisms of the net landward flow in the deeper waters of stratified estuaries. Rogers (1940), for example, suggested that larvae of rainbow smelt *Osmerus mordax* were retained in a stratified estuary through a mechanism of vertical migration, but were transported out of the system in another, intensively flushed, estuary. Thus, specific behavior patterns and estuarine hydrography may interact to retain larvae or plankton within estuaries. The hypothesis of vertical migration based upon a tidal rhythm (shallow at flood, deep at ebb) suggested by Carriker (1951) has been confirmed by Cronin and Forward (1979) for larvae of the crab *Rhithropanopeus harrisii*.

Among the least understood mechanisms of transport associated with estuaries is the one used by species that spawn offshore and subsequently enter estuarine systems as late larvae or early juveniles. These larvae must first move to nearshore areas, then locate an estuary mouth, and finally move into the estuary. This phenomenon is related to, but distinct from, retention in estuaries; it depends upon physical factors but is linked to active behavioral responses on the part of larvae. Movements to the nearshore environment from offshore are generally considered to be either passive or some form of modulated transport; in the latter case, behavioral attributes such as vertical migration or residence in convergences associated with internal waves play a role in movement (Shanks 1983; Kingsford and Choate 1986). Fishes spawning in the same offshore habitat may ultimately have different larval distributions, suggesting that small behavioral differences among species may alter susceptibility to passive transport (Powles 1981). The groups using estuaries typically are transported by drift to the nearshore environment (Rothlisberg et al. 1983; Miller et al. 1984; Boehlert and Mundy 1987). Nelson et al. (1977), for example, suggested that wind-driven Ekman transport is the mechanism of movement to the nearshore area, and that interannual variability in transport ultimately leads to variation in year-class strength.

Although movement to nearshore areas may be passive, the overwhelming evidence from both experimental and field work is that immigration of early life stages into the estuary is an active behavioral process. Such evidence exists for a variety of fish families, including anguillids (Creutzberg 1961; McCleave and Kleckner 1982), sparids (Pollock et al. 1983; Tanaka 1985), sciaenids (Weinstein et al. 1980), bothids (Weinstein et al. 1980), pleuronectids (Creutzberg et al. 1978; Tsuruta 1978; Rijnsdorp et al. 1985; Boehlert and Mundy 1987), and albulids (Pfeiler 1984). Still, the behavioral responses to physical factors influencing estuarine recruitment are poorly understood for the majority of taxa. In this paper, we consider the evidence for behaviorally mediated entry into estuarine nursery areas as a function of physical factors.

## Physical Factors Influencing Estuarine Recruitment

We recognize two major phases of movement necessary for recruitment to estuaries by species spawned offshore. The first is accumulation of larvae in the nearshore or coastal zone as described for Atlantic coast fishes by Nelson et al. (1977) and Miller et al. (1984); the second is the process of accumulation near inlets and estuary mouths and eventual passage through them. Each process involves a distinct set of physical factors to which the larvae respond and thus a distinct set of behaviors needed by the larvae to reach their optimum environment.

### *Nearshore Accumulation*

Accumulation in the nearshore zone is essentially passive, because larvae at this stage are typically planktonic; directed vertical movements, however, may modulate this transport to maximize shoreward movement. Accumulation can be prolonged, because many species are near ages of 60–90 d when immigration to estuaries occurs (Rosenberg 1982; Miller et al. 1984), and the youngest larvae are generally found most distant from the nearshore zone (Miller et al. 1984). Behaviors associated with shoreward movement are likely related to distribution in the water column and have evolved to take advantage of mean current conditions in the species' habitat. Behavioral differences between species can result in different distributions. Richardson and Pearcy (1977), for example, described coastal (0–28 km) and offshore (beyond 28 km) assemblages of ichthyoplankton that are persistent from year to year along the Oregon coast. Many species in the offshore assemblage are spawned along the coast, in some cases in the same season as species that remain in the nearshore assemblage. The species within these two groups show clear differences in their use of estuaries (Table 1). Thus, passive movements by larvae must be modulated by a behavioral component that, under mean conditions, results in the observed distributions.

Surface drift has been implicated in many studies of planktonic distribution, but the evidence from larval distributions is not always clear. The physical environment of the Atlantic menhaden *Brevoortia tyrannus*, including the surface and bottom currents, was investigated in the Chesapeake Bight by Harrison et al. (1967), who concluded that benthic orientation of larvae and their occurrence in deep water could result in passive transport to the mouth of Chesapeake Bay. Nelson et al. (1977), however, suggested that surface drift from Ekman transport was the operating transport mechanism. Later studies suggested an even more complex picture; Miller et al. (1984) proposed that both surface and bottom waters move offshore in winter months but that midlevel waters move onshore. Abundance of Atlantic menhaden larvae does not differ between deep and shallow water (Kendall and Reintjes 1975); thus a midwater distribution and avoidance of the surface and bottom offshore transport layers may result in onshore transport.

Other evidence exists for the importance of surface water transport. Early life stages of the English sole *Parophrys vetulus*, one of the few fish species on the west coast of North America that spawns offshore and uses estuaries as nursery grounds (Krygier and Pearcy 1986), are members of the nearshore ichthyoplankton assemblage (Richardson and Pearcy 1977; Mundy 1984). Recruitment to estuaries occurs on night flood tides for fish already beginning morphological transformation. A negative correlation exists between recruitment pulses of early stage larvae and the upwelling index (Figure 1). Larvae in early stages of transformation typically enter the estuary throughout the water column, whereas later-stage larvae arrive deeper in the water column. The correlation with the upwelling index is strong for

TABLE 1.—Selected species of fish larvae collected in abundance from Oregon marine waters (Richardson and Pearcy 1977), classified by distribution, by abundance in Yaquina Bay, Oregon, and by stage of development when found in the bay. Asterisks indicate species using the bay as a nursery. Distribution categories were modified from Richardson and Pearcy (1977); taxa categorized as "bay" include those found to be abundant by Pearcy and Myers (1974) and Mundy and Boehlert (unpublished data).

| Distribution | Abundance in Yaquina Bay | Species | Developmental stage in Yaquina Bay |
|---|---|---|---|
| Offshore | Absent | *Tarletonbeania crenularis* | |
| | | *Microstomus pacificus* | |
| | Rare | *Engraulis mordax* | Postflexion |
| | | *Stenobrachius leucopsarus* | Preflexion |
| | | *Glyptocephalus zachirus* | Preflexion |
| | Common | *Sebastes* spp. | Preflexion |
| Offshore and coastal | Common | *Hemilepidotus hemilepidotus* | Preflexion |
| Coastal | Absent | *Radulinus asprellus* | Preflexion |
| | Rare | *Microgadus proximus* | Preflexion, flexion |
| | | *Isopsetta isolepis* | Preflexion |
| | | *Platichthys stellatus* | Pre- to postflexion |
| | Common | *Clinocottus acuticeps* | Pre- to postflexion |
| | | *Psettichthys melanostictus* | Postflexion |
| | Abundant | *Clupea harengus pallasi** | Pre- to postflexion |
| | | Osmeridae | Pre- to postflexion |
| | | *Anoplarchus* spp.* | Pre- to postflexion |
| | | *Pholis* spp.* | Pre- to postflexion |
| | | *Enophrys bison** | Pre- to postflexion |
| | | *Leptocottus armatus** | Pre- to posflexion |
| | | *Parophrys vetulus** | Preflexion (few), postflexion |
| | | *Cottus asper**(?) | Pre- to postflexion |
| Bay only | Rare | *Apodichthys flavidus**(?) | Pre- to postflexion |
| | Common | *Gobiesox maeandricus** | Pre- to postflexion |
| | | *Ascelichthys rhodorus** | Preflexion |
| | Abundant | *Lepidogobius lepidus** | Preflexion to ? |

the abundance of surface-captured early larvae, but weak for numbers of deep-captured late larvae (Figure 1). Boehlert and Mundy (1987) suggested that early larvae were moving inshore along the entire coast during periods of onshore transport. Transforming larvae of English sole are present in the neuston and depend upon surface Ekman transport to arrive at the nearshore zone; sampling with large neuston nets has shown relatively high densities of transforming larvae of this species in the upper meter during months of peak recruitment (Shenker 1985). In contrast, late larvae enter the estuary along the bottom; they apparently recruit first to nearshore habitats, then migrate to the estuary mouth (Krygier and Pearcy 1986; Boehlert and Mundy 1987). The mean current patterns on the west coast may have resulted in the evolution of reproductive patterns such that most fish species spawn in the winter and early spring months when onshore surface transport dominates (Parrish et al. 1981). Deviations from the mean pattern of surface water transport may result in poor year-class strengths for species such as the Pacific hake *Merluccius productus* (Bailey 1981).

Several other mechanisms have also been proposed for movement to the nearshore zone, including population maintenance in eddies (Sale 1970). Eddy mechanisms have typically been used to explain the maintenance of populations associated with islands (Boden 1952; Emery 1972), but coastal studies off California suggest that eddy mechanisms might be important there as well (Hewitt 1981; Owen 1981). Population maintenance in the nearshore zone in an upwelling area may also be accomplished by use of countercurrent systems, whereby drift is modulated by changes in vertical distribution (Peterson et al. 1979; Wroblewski 1982; Figure 2). Such a mechanism, termed "larval navigation" by Crisp (1974), could maintain the nearshore ichthyoplankton assemblage noted off Oregon. Finally,

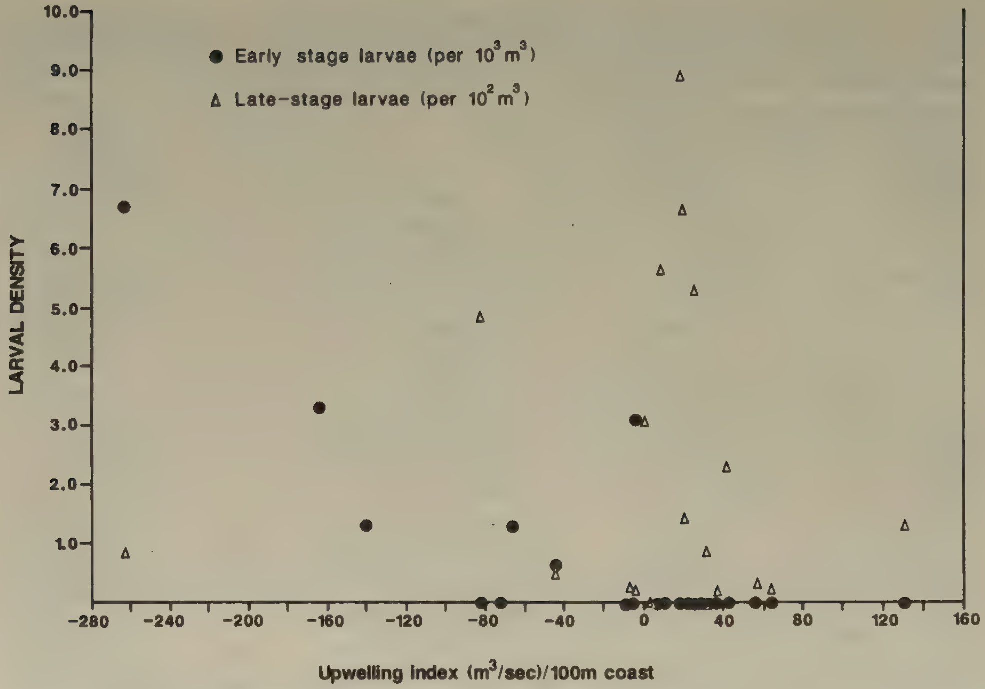

FIGURE 1.—Density of transforming larvae of English sole recruiting to Yaquina Bay, Oregon, as a function of the upwelling index. Early-stage larvae were taken by shallow nets; late-stage larvae were caught in nets set near the bottom, where these larvae are in higher abundance. Early larvae are abundant only during those times when the upwelling index is negative, suggesting onshore Ekman transport.

actual inshore movement may be modulated by accumulation in surface slicks, which in turn may be associated with internal waves (Shanks 1983, 1985; Kingsford and Choate 1986). Norris (1963) suggested a behavioral mechanism of orientation to these slicks; avoidance of the lower temperature at internal wave fronts by young opaleyes *Girella nigricans* would facilitate shoreward movement.

### *Estuarine Recruitment*

Once larvae have recruited to the nearshore environment, a new set of physical factors influence their accumulation at inlets or estuarine mouths and their movements upstream into the estuary. Alongshore drift must play a key role in the movement of larvae to areas under estuarine influence. This influence may be more important on the west coast of North America, where only 10–20% of the coast is estuarine, than along the Atlantic and Gulf of Mexico coasts, which are 80% estuarine (Emery 1967). Krygier and Pearcy (1986) observed increases in the density of larval English sole in a nearshore nursery area distant from any estuarine influence. As densities at that location decreased, however, densities in Yaquina Bay, some 10 km to the south, increased, demonstrating a linkage between the nearshore and estuarine nursery areas. A southern alongshore drift may have brought the larvae near the estuarine mouth. The transition from northward to southward alongshore drift off Oregon typically occurs during March (Huyer et al. 1975), a period when the metamorphosing larvae enter Yaquina Bay (Krygier and Pearcy 1986; Boehlert and Mundy 1987).

Several physical factors near inlets or estuaries may serve as "point source" stimuli that could elicit short-term behavioral responses by larvae. Tidal flux may ultimately lead to accumulation, but tidal flux is a complex of related factors that cannot be isolated in field studies. This complex includes current speed, salinity (as affected by both river discharge and magnitude of tidal mixing and exchange), temperature, olfactory cues, turbidity, bottom composition (grain size), and lunar

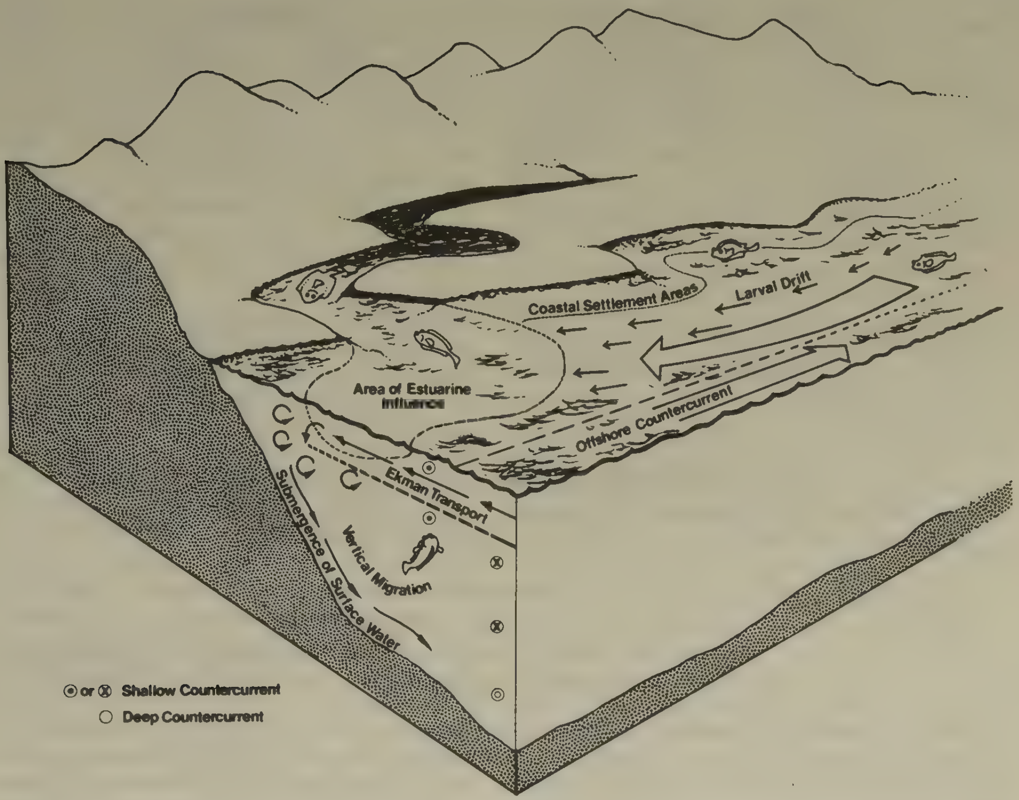

FIGURE 2.—Diagramatic representation of movements of larval fishes in the Oregon upwelling zone. Pelagic larvae may control onshore–offshore transport by their vertical movements, using surface Ekman transport to move shoreward (this condition pertains during the winter season off the Oregon coast). After larvae move near shore and settle, alongshore transport may result in movement to areas under estuarine influence.

phase. Individually and in concert, each factor may play a role in altering larval behavior patterns that facilitate recruitment. The complexity was pointed out by Hoar (1953), who suggested that "more rapid progress might be made if migrations which are not complicated by changes in osmotic medium are studied."

Many authors, including those cited previously, have monitored both recruitment to and maintenance in estuaries for a variety of taxa; results of these studies often are complex. Weinstein et al. (1980), who conducted one of the most detailed sampling studies, monitored movement of some commercially important species in an inlet in North Carolina. Catches of flounder *Paralichthys* spp. were greater on flood tides, particularly at night, which led the authors to suggest that the flounder postlarvae moved to the bottom during ebb tides. At night flood tides, flounders and spot *Leiostomus xanthurus* occurred high in the water column. Weinstein et al. (1980) suggested that this mechanism transported these two taxa to the tidal flats and creeks, which they used as nursery areas (Shenker and Dean 1979; Weinstein 1979, 1983). In contrast, postlarvae of Atlantic croaker *Micropogonias undulatus*, which use the head of the estuary, remained deeper in the water column, even at night. The model devised by Weinstein et al. (1980) may be used to explain both recruitment to and maintenance in estuaries (Figure 3); their results clearly show that species-specific behavioral responses to physical factors may result in different distributions within the estuary.

A suite of physical factors may serve as cues for such behavior. Several authors have investigated the relationship of animal distribution in the field to salinity and also the behavior of fish in laboratory tanks as a function of salinity. Many studies

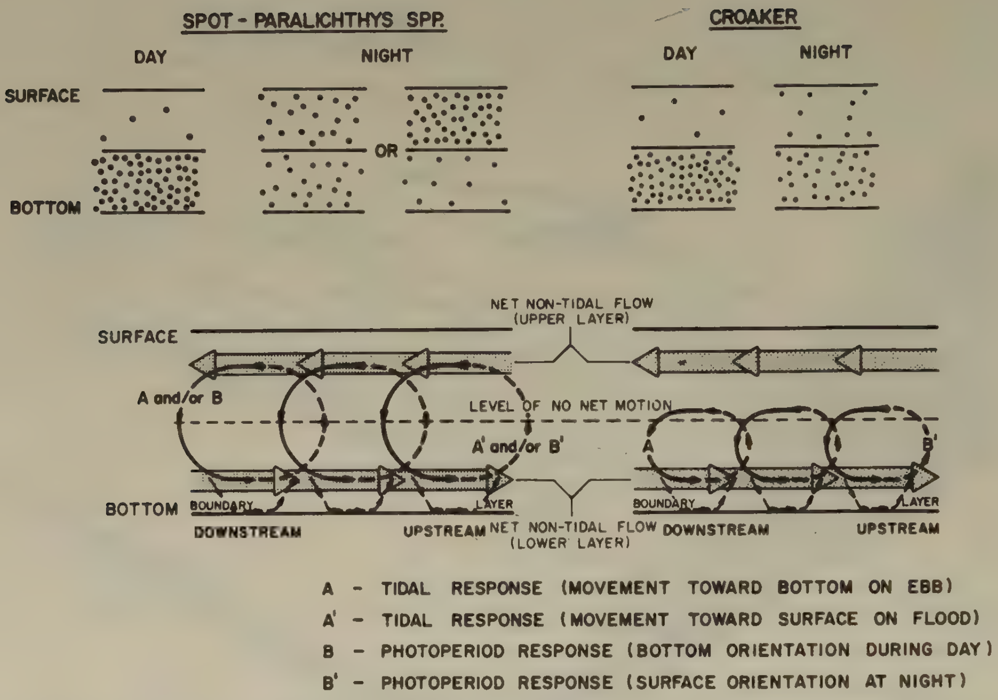
SPOT - PARALICHTHYS SPP.
DAY
NIGHT
SURFACE
BOTTOM
OR
CROAKER
DAY
NIGHT
NET NON-TIDAL FLOW (UPPER LAYER)
SURFACE
A and/or B
LEVEL OF NO NET MOTION
A' and/or B'
A
B'
BOTTOM
BOUNDARY LAYER
BOUNDARY LAYER
DOWNSTREAM
UPSTREAM
NET NON-TIDAL FLOW (LOWER LAYER)
DOWNSTREAM
UPSTREAM
A - TIDAL RESPONSE (MOVEMENT TOWARD BOTTOM ON EBB)
A' - TIDAL RESPONSE (MOVEMENT TOWARD SURFACE ON FLOOD)
B - PHOTOPERIOD RESPONSE (BOTTOM ORIENTATION DURING DAY)
B' - PHOTOPERIOD RESPONSE (SURFACE ORIENTATION AT NIGHT)

FIGURE 3.—A model of movements with the tide for three taxa of postlarval fishes in a North Carolina estuary, showing different strategies of tidal-stream transport. Spot and flounders use shallow tidal areas, whereas Atlantic croakers move to the upper reaches of the estuary, presumably by remaining deep in the water column at all times. (From Weinstein et al. 1980.)

have been based upon the classic work of Creutzberg (1961), who studied the immigration of European eel elvers *Anguilla anguilla* to tidal areas from the open sea. Field sampling demonstrated that the elvers swam actively in the water column on flood tides, but they were either near bottom or clinging to the bottom during ebb tides; this behavior pattern resulted in inshore movement. Creutzberg investigated the behavioral responses to increasing and decreasing salinity, but with "disappointing" results. More recent studies, particularly those with crustaceans, show clear responses to changes in salinity. Postlarval penaeid shrimp *Penaeus duorarum* move into estuarine nursery areas, whereas juveniles move out. Direct salinity changes, rather than some other factor, caused changes in behavior that resulted in the appropriate movements. Decreasing salinity caused benthic orientation by postlarvae and negative rheotaxis by juveniles; increasing salinity resulted in swimming behavior by the postlarvae but positive rheotaxis by the juveniles (Hughes 1969). The importance of salinity in determining the use of estuarine nursery areas by young shrimp is dramatically demonstrated by the strong correlation of offshore commercial shrimp catch with rainfall in the preceding year. Years with low rainfall have low salinity change near the estuaries and recruitment of postlarvae to estuaries is less successful. Salinity was also suggested as the controlling factor for emigration of the swimming crab *Macropipus holsatus* from estuarine areas (Venema and Creutzberg 1973); as with the juvenile shrimp, the crabs swim during decreasing salinity and settle to the bottom during times of increasing salinity, resulting in seaward movement. Physical variables are often highly intercorrelated, however, and speculations of causal relationships in such cases may be spurious. In our work with English sole, for example, there was a strong negative correlation between bottom salinity at the start of a flood tide and density of larvae recruiting to an estuary (Boehlert and Mundy 1987). Bottom salinity was highly correlated with other physical factors, however, including freshwater input, sea level, surface salinity, surface temperature, and other factors that may be related to recruitment. When larvae migrate onto nonestuarine tidal flats, they may encounter only very slight salinity differences, as in Elkhorn Slough, California (Yoklavich 1982), in the Gulf of Carpenteria, Australia (Staples 1980), or in some tropical areas (Pfeiler 1984). In the tropics, increased salinity caused by evaporation in hypersaline lagoons may allow salinity gradients to develop, but the salinity change is opposite that in estuarine systems. One must thus use caution in interpreting cause and effect in relationships between recruitment and single physical factors.

Temperature gradients between estuarine and offshore waters may be strong in temperate regions, particularly in winter months. Temperature is a candidate physical orientation factor for larvae because fish show temperature tolerances and preferences (Brett 1970). The majority of studies of temperature and migration, however, describe temperature-initiated migration out of an area. Hoar (1951), for example, showed that increasing temperature causes a change from positive to negative rheotaxis by young salmonids *Oncorhynchus* spp., facilitating downstream migration. Olla et al. (1980) showed that the tautog *Tautoga onitis* migrates to deeper water as temperature increases. Animals moving into estuaries might be seeking a preferred temperature, but more research is needed before any role of temperature in recruitment can be understood.

Other cues associated with water chemistry may play important orientation roles. Creutzberg's "disappointing" results with European eel elvers occurred when he altered salinity with tap water and observed no response, but when he diluted seawater with natural inland waters the elvers showed swimming behavior during increasing salinity and benthic orientation during decreasing salinity. Creutzberg (1961) suggested that some "attractive substance" in inland waters was the important factor in the immigration, rather than salinity alone. These results were later confirmed by Miles (1968) with elvers of the American eel *Anguilla rostrata*. He observed that some biodegradable component of either dissolved or particulate organic matter played a role. Thus some unknown "inland water odor," sensed through olfaction and similar to home-stream odors detected by adult salmonids (Hasler et al. 1978), may be involved. An alternative, but related, "odor" hypothesis is that a species- or population-specific pheromone may be involved (Nordeng 1977), but little evidence exists for this hypothesis.

Another olfactory cue is food odor, which may trigger activity if predatory larvae are unsatiated. Research on the movements of larval plaice *Pleuronectes platessa* in tidal areas showed that larvae were three times as abundant in the water column on flood than on ebb tides, resulting in net inshore transport (Creutzberg et al. 1978). Preliminary experimental data, however, suggested a mechanism of immigration different from that of other species studied. In the laboratory, neither salinity nor nursery "odors" stimulated behavior appropriate for transport, but starved animals exhibited greater swimming activity in the water column than fed animals. Although Creutzberg et al. (1978) proposed that tidal areas act as "traps" due to the abundance of food (as compared to offshore areas), they could not explain the stimulus for settlement. Gradients of food abundance may play a role in accumulation of young fish; Tanaka (1985) suggested that a gradient of copepod abundance, increasing from offshore to inshore, could lead immigrating red sea bream *Pagrus major* to inshore areas where the preferred prey, gammaridean amphipods, are present. Larval Atlantic herring *Clupea harengus harengus* may show vertical distributions within estuaries that are adaptive for population maintenance, but Fortier and Leggett (1983) suggested that these movements are simply a behavioral response to vertical movements of their prey organisms.

A variety of other candidate physical factors exist near entrances to estuaries that may elicit behavior appropriate for recruitment. Currents, a dominant feature of tidal flux, may be used, but only by fishes able to orient to a surface. Rheotaxis by young salmonids, for example, is lost in darkness, resulting in downstream movements (Hoar 1958). Transforming plaice, on the other hand, show different rheotactic responses depending upon their distance from a solid surface; within 3 cm of the surface, they are able to show normal rheotaxis even in darkness, but at greater distances they lose the ability to orient (Arnold 1969).

The use of electric or magnetic fields for orientation by fish larvae has not yet been demonstrated, but the elvers of American eels can detect relatively weak electric fields (McCleave and Power 1978). The thresholds for detection may be such that the relatively strong water currents (which cause electric fields) in regions of high tidal flux could be used for orientation. If this were the case, there would be no need for visual or tactile contact with the bottom, as discussed above with respect to rheotaxis.

Turbulence, turbidity, and light may interact to affect distributions. Fore and Baxter (1972) suggested that larval Atlantic menhaden seek less turbulent water and thereby accumulate in shallows and tidal creeks. In contrast, Blaber and Blaber (1980) observed the highest densities of juvenile fishes in the most turbid reaches of estuaries; negative phototropism may be involved in accumulation in such areas. Residence in turbid areas may result in decreased predation (Moore and Moore 1976; Gardner 1981). Some larvae, such as those of Pacific herring *Clupea harengus pallasi,* may indeed be adapted for feeding and survival in turbid estuaries (Boehlert and Morgan 1985). Rijnsdorp et al. (1985) suggested another relationship with turbulence; they observed a high correlation of suspended matter with the abundance of immigrating plaice larvae, suggesting that larvae may be swept up by stronger tides along with suspended materials. Flood tides at their study sites were typically stronger than the ebb tides, so their observations suggest that passive transport alone, with no behavioral change, could be important for immigration. Working with the young larvae of Atlantic herring, however, Fortier and Leggett (1983) noted no overall vertical dispersion during times of greatest vertical mixing of an estuary, contrary to the expectation that larvae would be passively mixed by turbulence (Fortier and Leggett 1982).

Lunar phase may affect transport of larvae into estuaries, but the mechanism is unknown. From a long-term study, Williams and Deubler (1968) suggested that lunar phase affects the timing of entry into estuaries for *Paralichthys* postlarvae and also for postlarval penaeid shrimps *Penaeus duorarum;* both groups were captured in greater numbers near the times of new moons than of full moons. This was later confirmed for penaeid shrimps by Roessler and Rehrer (1971). Similarly, catches of *Anguilla* elvers may show lunar periodicities (Jellyman 1979; Tzeng 1985). Tzeng (1985) obtained peak catches of riverine elvers at both new and full moons, correlated with spring tides. In coastal waters, however, peak catches occurred only during the new moon, suggesting that light inhibited activity there (Tzeng 1985). In all these studies, net avoidance is a confounding factor that may decrease catches during full moon. We observed no lunar periodicity in the immigration of larval English soles to Yaquina Bay, Oregon (Boehlert and Mundy 1987). Lunar phase is also coupled to changing tidal magnitude and, therefore, to salinity and temperature changes, current speed, and turbulence. Field or laboratory studies designed specifically to test hypotheses about the interrelationships among physical factors affecting immigration rates would be necessary to determine the roles of these physical factors.

### Behavioral Responses to Estuarine Stimuli

The ability of organisms to orient to environmental stimuli underlies their movement to and retention in habitats that are optimal for survival. Aquatic organisms that inhabit different environments during ontogenetic development must respond to changing stimuli to orient to each new habitat. Recruitment to estuaries, we believe, is a behaviorally mediated rather than passive migration. To investigate migration, Hoar (1953) suggested that research " . . . should start with the behavior patterns of the fish; it should involve an analysis of the internal physiological states responsible for this restless appetitive behavior, and eventually, an understanding of the way in which this activity is guided and directed by the variables in the external environment." Behavior has generally been inferred from distribution in the field (changes in abundance), and correlation or statistical approaches have been used to relate results to physical variables. The appetitive behaviors necessary for recruitment may begin as either random movements (kineses) or directed movements (taxes). Organisms may accumulate during kinesis by changing rates of activity or rates of turning (Hunter and Thomas 1974) and during taxis by slowing movement when they reach the source of a directional stimulus. There are relatively few physical factors with vector properties; therefore, directed movements may be limited to phototaxis, geotaxis, and rheotaxis in response to light direction, gravity, and currents, respectively (Crisp 1974). Each of these factors might guide estuarine immigration, but they must be modulated by scalar factors such as salinity, temperature, turbidity, and olfactory cues; sequential sampling of a scalar factor through time or space may allow development of a directional sense through a learned response. These more advanced behavioral sequences, however, may be beyond the physical and sensory capability of larval or juvenile fishes, because current speeds in tidal inlets may prevent young fishes from controlling their horizontal position.

Tidal-stream transport is commonly cited as an example of vertical movement affecting horizontal displacement (Tsuruta 1978; Weinstein et al.

1980). Generally, the control of larval vertical distribution may arise either through taxis or kinesis. Fish larvae are frequently concentrated near thermoclines (Ahlstrom 1959; Loeb 1979), and kineses may explain accumulation over time within specific thermal regimes. Kinetic motion may be the most efficient way for larvae to find food under some circumstances (Hunter and Thomas 1974). Random kinetic motions cannot accomplish directed vertical movements, which must, therefore, be associated with a taxis or (as suggested by Fortier and Leggett 1983) with feeding excursions. No single mechanism has yet emerged as a general control of vertical placement for tidal-stream transport. Phototaxis of fish larvae has been documented extensively in the field and laboratory (Ahlstrom 1959; Blaxter and Staines 1970; Blaxter 1974; Hunter and Sanchez 1976; Kendall and Naplin 1981; Yamashita et al. 1985), but it typically operates on diel cycles. Reaction to both direction and intensity of light may explain the presence of immigrating larvae in night rather than day flood tides (Weinstein et al. 1980; Boehlert and Mundy 1987), but it cannot provide the temporal cue for activity on flood and not ebb tides. Similarly, geotaxis cannot account for observed periodicities in activity by larvae.

Rheotaxis of fishes plays an important part in tidal-stream transport; the subject has been reviewed by Arnold (1974, 1981). Fish can apparently detect current speeds of 1–10 cm/s (Arnold 1981), which are within or below the range of tidal currents, and the lateral line system, which detects water movements, develops relatively early in fish larvae (Iwai 1967). Thus, young fish may use currents and rheotaxis for recruitment to an estuary. This use is constrained by the need for either visual or tactile contact (Arnold 1969), as described earlier. Tidally generated turbulent fields within estuaries, however, may provide tactile cues under certain conditions (McCleave and Kleckner 1982).

### Development and Behavioral Ontogeny in Relation to Movements

The stage of development at which fishes are present in inlets or estuaries may in large part determine their ability to behaviorally alter their distribution. For species spawned within an estuary, early larvae may be advected out, particularly from intensively flushed estuaries (Rogers 1940; Johnson and Gonor 1982). For those species using the estuary for a nursery, development may continue in offshore waters; Pacific herring, for example, are abundant in estuaries at certain times of year (Pearcy and Myers 1974), but they are also found in the nearshore assemblage of ichthyoplankton (Richardson and Pearcy 1977; Table 1). Resident species may be temporarily exported only to return to the estuary at a later stage (Johnson and Gonor 1982). In general, species that recruit to estuaries from offshore do so at advanced developmental stages, usually near or after metamorphosis; this is true for several orders of fishes, including Anguilliformes (Creutzberg 1961), Elopiformes (Pfeiler 1984), Clupeiformes (Miller et al. 1984), Perciformes (Weinstein et al. 1980; Tanaka 1985), and Pleuronectiformes (Tsuruta 1978; Boehlert and Mundy 1987).

Important changes occur at metamorphosis in sensory systems, behavior, and morphology that affect immigration to estuaries. Metamorphosis entails full development of fins and associated structural calcification, which result in better swimming capabilities (Blaxter and Staines 1971). Fukuhara (1985), for example, noted an increase in swimming speed of red sea bream from 1 body length/s for larvae to 4 body lengths/s for metamorphosed juveniles. Greater swimming ability may decrease a larva's chance of being flushed from the estuary, even during times of high freshwater input (Rogers et al. 1984). Many species undergo rapid changes in color and morphology in association with the change from pelagic to benthic existence (Hubbs 1958; Hunter 1967; Kendall et al. 1984). Major changes in structure and function of the retina occur (Blaxter 1974; Boehlert 1978; Kawamura and Hara 1980), including development of rods in the retina (Blaxter 1974) that are necessary for vision in dim light. Flatfish larvae undergo great changes in behavior at the time of metamorphosis (Fluchter 1965; Finger 1976; Gibson et al. 1978); they become benthic, and their rheotactic behavior effectively ceases (Arnold 1969). Kawamura and Ishida (1985) gave a detailed account of the changes in sensory systems and behavior from hatching to 72 d posthatch for the flounder *Paralichthys olivaceus*. In particular, they noted development of retinal rods at 25 d, disappearance of positive phototaxis at 30 d, and nocturnal activity at 33 d posthatch. It is during this 9-d period that the transition from the pelagic to benthic habitat occurs. Pfeiler (1984) described changes during metamorphosis of bonefish *Albula* sp., which shrink 60–65% as they enter hypersaline lagoons.

Generalizations about the methods of immigration for different fishes are difficult, but we wish to distinguish between perciform, anguilliform, and pleuronectiform fishes. Tanaka (1985) suggested that tidal-stream transport, which is important to flatfish and eels (Creutzberg 1961; Tsuruta 1978; McCleave and Kleckner 1982), is of secondary importance to perciform juveniles, which have more advanced swimming abilities but, perhaps more importantly, no ability to settle on the bottom. As they near metamorphosis, larval plaice and flatfish generally spend increasing amounts of time near the bottom, often alternating pelagic and benthic behavior (Fluchter 1965; Blaxter and Staines 1971). Given the proper behavior patterns with respect to tidal movements, these larvae could immigrate inshore using tidal-stream transport during flood tides and settling on the bottom during ebb tides; the energetic savings of this mode of migration approach 90% for juvenile fish (Weihs 1978). Blaxter and Staines (1971) observed that when larval plaice metamorphosed, their movement rates dropped from about 70 to 4 cm/min, the time they spent actively swimming changed from 95 to 10%, and the volume of water they searched (for food) dropped from 2,500 to 50 mL/h. This is a clear distinction from the changes noted above for red sea bream, a perciform (Fukuhara 1985). Although perciform fish use tidal stream transport (Weinstein et al. 1980), the benefits may be relatively low due to their inability to settle out on the bottom.

Relatively little work has been done on the influence of habitat type on larval settlement. Certain species may be able to delay transformation until they encounter suitable juvenile habitat (Pearcy et al. 1977; Moser 1981); this has recently been demonstrated, based on daily growth increments, for a coral reef fish (Victor 1986). Marliave (1977) found significant substrate preferences by settling larvae in five of six benthic species tested. The preferences seemed to be for structural features of the substrate that gave tactile cues to the settling larvae. Metamorphosing flatfish alternate between pelagic swimming and benthic resting behavior (Fluchter 1965), a behavior that may aid settling larvae in locating preferred habitats.

### Role of Endogenous Rhythms

Another behavioral consideration important in recruitment to estuarine nursery areas is endogenous activity rhythms. As already noted, many of the physical factors associated with tidal flux have clear temporal signals but lack directionality. Temporal cues, or "zeitgebers," exist for setting internal clocks for individuals in nearshore areas under the influence of an estuarine system. A wide variety of evidence supports the presence of endogenous rhythms in fishes (see Thorpe 1978), including studies of activity patterns (Gibson 1965), retinomotor movements (Olla and Marchoni 1968), photosensitivity (Davis 1962), and biochemical patterns (de Bras 1979). The actual timekeeping mechanism may be a chemical phenomenon mediated by the pineal gland (Binkley et al. 1978; Matty 1978).

Endogenous rhythms may be daily, tidal, or lunar in periodicity. They can be observed experimentally, in the absence of temporal stimuli, for varying periods before they revert to a free-running rhythm. They are synchronized by normal environmental cycles to the appropriate periodicity (Enright 1975). Within species, endogenous rhythms may change during ontogeny. Planktonic plaice larvae are most active near the surface at night, but the rhythmicity is a function of light, rather than of any endogenous rhythm, because it disappears in constant light or darkness (Gibson et al. 1978). After planktonic larvae undergo a short period of relatively little activity (Blaxter and Staines 1971) and settle, newly benthic larvae maintain diel activity peaks. Populations remaining offshore retain this diel pattern, but nearshore or estuarine populations exhibit marked tidal activity patterns that are often of an endogenous nature (Gibson 1978; Gibson et al. 1978). That these rhythms change with changing habitat suggests that they may play an important role in habitat selection.

Endogenous rhythms in general were reviewed by Enright (1975); tidal rhythms have been reviewed by Palmer (1973) and Gibson (1978). Tidal rhythms generally relate to activities important for foraging, respiration, and movement and to other activities affected by tidal cycles. Tidal rhythms have been demonstrated for many species of fishes (Gibson 1978). The entrainment of the circatidal rhythm must occur after young fish come under the influence of estuaries in nearshore waters. Appropriate zeitgebers for synchronizing circatidal rhythms include pressure (Gibson 1971) and turbulence (Enright 1965) and, possibly, inundation and temperature (Palmer 1973). Cyclic changes in salinity in estuarine areas could also act as a zeitgeber. It is important that rhythms are set by local conditions, because tides differ in magnitude and phase over the range of most species. Some species such as the English sole may use different cues in different areas, because some estuaries they occupy have freshwater inputs and others have nearly none (Yoklavich 1982; Boehlert and Mundy 1987). If such species develop endogenous rhythms as they immigrate to estuaries, it is likely that the suite of physical factors associated with tidal flux, rather than a single factor, may serve as the zeitgeber. This is supported by the lack of a conclusive experimental identification of the zeitgeber for a tidal rhythm. Also, laboratory-reared animals have circadian rhythms instead of the circatidal rhythms found in field-collected animals of the same species (Gibson et al. 1978; Cronin and Forward 1979, 1983).

Hughes (1972) demonstrated endogenous, circatidal rhythms of swimming by the shrimp *Penaeus duorarum* over 3 d under constant conditions; he suggested that the postlarval shrimp were pelagic, drifting with the current during flood tide but exhibiting benthic behavior during ebb, resulting in movement into and up the estuary, much in the way described for fish by Weinstein et al. (1980; Figure 3). The significance of such a circatidal rhythm is obvious; if a single cue such as salinity or odor is used as a stimulus for pelagic or benthic behavior, there is no mechanism for the animal to detect the end of flood tide (McCleave and Kleckner 1982). Because the drifting animal will remain in the same water mass until it mixes with ebbing water, considerable downstream transport may occur. Linking the behavioral pattern to a circatidal rhythm would allow the animal to settle from the water column at the end of flood tide in the absence of stimuli associated with water quality, resulting in more efficient migration. Such rhythms must play a key role in tidal stream transport.

### Behavioral Model of Recruitment to Estuaries

In studies of fish recruitment to estuaries, researchers typically consider spatial and temporal patterns of distribution and correlate them with a wide range of physical variables to infer the behavioral responses by the immigrating fish (Tsuruta 1978; Boehlert and Mundy 1987). In the laboratory, however, effects of physical factors generally are considered in isolation (Creutzberg 1961), often with somewhat surprising or enigmatic results (Creutzberg et al. 1978). Problems may arise due to artifacts associated with the laboratory environment, as shown by different behaviors of laboratory-reared and field-captured animals (Gibson et al. 1978; Cronin and Forward 1979, 1983). In this section, we consider a conceptual model for the behavior of fish and their responses to physical variables or other stimuli as they affect recruitment to estuaries. Such a model may be useful in the development of testable hypotheses.

Certain field studies have suggested mechanisms of estuarine recruitment that are entirely passive and require no behavioral response on the part of the larvae (Rijnsdorp et al. 1985). The majority of information on fishes, however, suggests otherwise. Most movements can be classified as a form of tidal-stream transport, and thus behavioral considerations associated with migration are pertinent, but we frame our model in terms of the process of habitat selection. Sale (1969) considered habitat selection as a negative feedback mechanism; stimuli from the environment, monitored by sense organs, feed into a "selection mechanism" which then triggers "appetitive exploration." In fishes, appetitive exploration may take many forms, from simple activity to changes in vertical distribution to rheotaxis or phototaxis. As a kinetic movement, such searching behavior may ultimately result in accumulation in more favorable environments where random activity will be reduced (Hunter and Thomas 1974). Sale suggested that in an adequate or optimal environment, the intensity of feedback is relatively low, which may eliminate or reduce appetitive exploration. In an inadequate environment, the feedback intensity increases, resulting in a greater percentage of the animal's time being spent in searching behaviors. Sale (1969) provided support for this hypothesis for habitat selection by showing that young manini *Acanthurus triostegus* reduce their exploratory behavior in an appropriate environment. Because fishes change optimal habitats with growth, the stimuli important for the "selection mechanism" most likely change throughout ontogeny as habitat requirements change. This was observed by Norris (1963) in a study of the selection of thermal habitats by opaleyes.

In the context of an estuarine system, Sale's model is more applicable than are simple concepts of taxes or kineses. The suite of physical factors is complex and, during ontogeny, larvae must select among several habitats. Our conceptual model (Figure 4) is generalized to allow application to a variety of species. We consider four habitats sequentially occupied by migrants; the dominant physical process in the habitat, the stimuli inducing the fishes' behavior, and the dominant activity pattern of the fish all determine the transition from

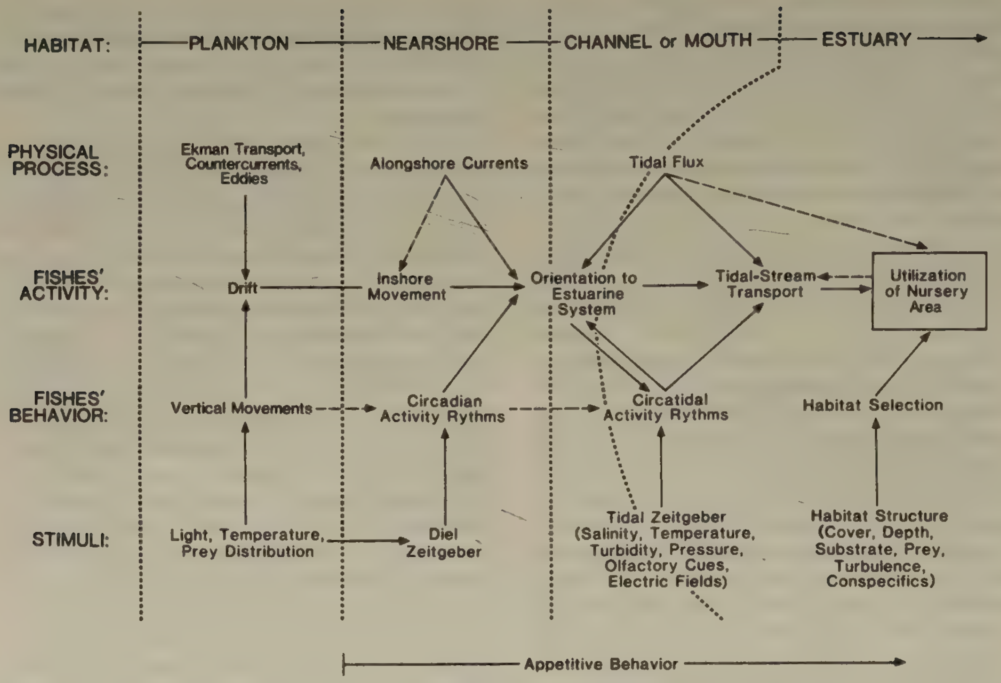
HABITAT:
PLANKTON
NEARSHORE
CHANNEL or MOUTH
ESTUARY
PHYSICAL PROCESS:
Ekman Transport, Countercurrents, Eddies
Alongshore Currents
Tidal Flux
FISHES' ACTIVITY:
Drift
Inshore Movement
Orientation to Estuarine System
Tidal-Stream Transport
Utilization of Nursery Area
FISHES' BEHAVIOR:
Vertical Movements
Circadian Activity Rythms
Circatidal Activity Rythms
Habitat Selection
STIMULI:
Light, Temperature, Prey Distribution
Diel Zeitgeber
Tidal Zeitgeber (Salinity, Temperature, Turbidity, Pressure, Olfactory Cues, Electric Fields)
Habitat Structure (Cover, Depth, Substrate, Prey, Turbulence, Conspecifics)
Appetitive Behavior

FIGURE 4.—A conceptual model for the role of stimuli and behavior in fish movement to estuarine nursery areas.

one habitat to the next. We first consider the offshore planktonic habitat, where the eggs and larvae are distributed. Here, the dominant physical factors are Ekman transport, countercurrents, and eddies (Parrish et al. 1981; Miller et al. 1984; Figure 2). Light, temperature, and prey distribution may be the key stimuli affecting vertical distribution, which may control the passive pattern of drift, both onshore–offshore and alongshore. This process may be one of critical importance to survival and one that may vary interannually, resulting in variations in year-class strength for both estuarine- and nonestuarine-dependent species (Nelson et al. 1977; Bailey 1981; Parrish et al. 1981).

Later larvae enter the phase of appetitive behavior as they begin searching for benthic habitat. A successful transition from the planktonic to the nearshore habitat involves "settlement," which may be taken literally in the case of a pleuronectiform but which may be referred to as "benthic orientation" for perciforms. In this initial settlement, substrate type and depth may be important factors (Marliave 1977). This is a major change usually involved with the process of metamorphosis. For species utilizing estuaries, the nearshore zone is a transitory habitat. Although we generally suggest that only late larvae recruit to the benthic nearshore habitat, more recent studies are documenting surprisingly large concentrations of various stages of fish larvae near bottom or rocky reefs (Brewer et al. 1981; Marliave 1986). Additional data may change our thinking about the process of recruitment to the nearshore zone. Later-stage larvae have increased powers of locomotion. At this stage, rhythmic activity may begin to play an important role in behavior and a circadian rhythm may develop (Gibson et al. 1978). Since the majority of fishes immigrate to estuaries at night (Pfeiler 1984; Tzeng 1985; Boehlert and Mundy 1987), it is probable that nocturnal activity is the rule; swimming activity, along with the movement induced by alongshore currents, may result in movement to the next transitory habitat, the channel or mouth of the estuary (the area of "estuarine influence" in Figure 2).

In Sale's (1969) hypothesis for habitat selection, the "intensity" of stimuli near the channel mouth would vary with a tidal periodicity. During ebb tides, settlement or bottom orientation might be induced by the factors associated with tidal flux (Figure 4), whereas the intensity of these stimuli would change during flood tides, as offshore water moves into the estuary. This condition would occur if a simple stimulus–response behavior exists. Such behavior patterns have been suggested for shrimp with salinity as the stimulus (Hughes 1969), for *Anguilla* elvers with "inland water odor" as the stimulus (Creutzberg 1961), and for plaice larvae with olfactory cues from prey as the stimulus (Creutzberg et al. 1978). Although such behavior would result in a form of tidal-stream transport, response to a single stimulus is a relatively simplistic mechanism and would not occur until a tidal change was well underway (McCleave and Kleckner 1982). Further, flow patterns around the mouths of estuaries are sufficiently complex to decrease the probability that a single factor changes consistently with a tidal periodicity (Ozsoy and Unluata 1982). Instead, we propose that a suite of stimuli associated with tidal flux acts as a zeitgeber to superimpose a circatidal rhythm upon the circadian rhythm which already may be present (O'Connor 1972; Gibson 1978). In this case, nocturnal swimming activity on flood tides and benthic orientation during other times could result in tidal-stream transport and movement up the estuary.

The process of estuarine recruitment may be a continuing one for some species that depend upon the process of habitat selection once inside the estuary (Figure 4). Weinstein et al. (1980) suggested that different vertical distribution patterns during tidal flux result in species-specific distributions within the estuary (Figure 3). The wide range of habitats present, and the new set of stimuli (vegetation, turbulence, prey distribution, substrate type) they provide, can lead to selection of shallow areas where flushing from the estuary is not a problem (Weinstein 1983; Rogers et al. 1984) or, conversely, to selection of areas near inlets where tidal-stream transport may be a continuing process necessary to maintain the fish within the estuary.

Sampling studies near the mouths of estuaries have provided a wealth of information on the movements of larval and juvenile fishes through inlets. Generally, these have led authors to generate hypothetical schemes of behavior involved in recruitment to and maintenance within estuaries. To date, laboratory studies (Creutzberg 1961; Miles 1968; Arnold 1969; Creutzberg et al. 1978; McCleave and Power 1978) on behavior of fishes relative to estuarine recruitment have tested some of the field-generated hypotheses on behavior, but they typically have used simplified designs that may not be meaningful to the field situation. More comprehensive studies on endogenous rhythms in fishes, including the array of zeitgebers as they relate to tidal-stream transport, are necessary; however, the behavioral complexity and activity patterns of fish larvae during transformation require that experimental facilities be larger than they have been so they can mimic natural environments.

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## References

Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish and Wildlife Service Fishery Bulletin 60:106–146.

Arnold, G. P. 1969. The orientation of plaice larvae *Pleuronectes platessa* in water currents. Journal of Experimental Biology 50:785–801.

Arnold, G. P. 1974. Rheotropism in fishes. Biological Reviews of the Cambridge Philosophical Society 49:515–576.

Arnold, G. P. 1981. Movements of fish in relation to water currents. Pages 55–80 *in* D. J. Aidley, editor. Animal migration. Cambridge University Press, London.

Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake, *Merluccius productus*. Marine Ecology Progress Series 6:1–9.

Binkley, S. A., J. B. Riebman, and K. M. Reilly. 1978. The pineal gland; a biological clock in vitro. Science (Washington, D.C.) 202:1198–1200.

Blaber, S. J. M., and T. G. Blaber. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17:143–162.

Blaxter, J. H. S. 1974. The eyes of larval fish. Pages 427–443 *in* M. A. Ali, editor. Vision in fishes. Plenum, New York.

Blaxter, J. H. S., and M. E. Staines. 1970. Pure cone retinae and retinomotor responses in larval teleosts. Journal of the Marine Biological Association of the United Kingdom. 50:449–460.

Blaxter, J. H. S., and M. E. Staines. 1971. Food searching potential in marine fish larvae. Pages 467–485 *in* D. J. Crisp, editor. Fourth European marine biological symposium. Cambridge University Press, Cambridge, England.

Boden, B. P. 1952. Natural conservation of insular plankton. Nature (London) 169:697–699.

Boehlert, G. W. 1978. Intraspecific evidence for the function of single and double cones in the teleost retina. Science (Washington, D.C.) 202:309–311.

Boehlert, G. W., and J. B. Morgan. 1985. Turbidity enhances feeding success of larval Pacific herring, *Clupea harengus pallasi*. Hydrobiologia 123: 161–170.

Boehlert, G. W., and B. C. Mundy. 1987. Recruitment dynamics of metamorphosing English sole, *Parophrys vetulus*, to Yaquina Bay, Oregon. Estuarine, Coastal and Shelf Science 25:261–281.

Bousfield, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. National Museum of Canada Bulletin 137.

Brett, J. R. 1970. Temperature—Pisces. Pages 515–560 *in* O. Kinne, editor. Marine ecology, volume 1. Wiley, New York.

Brewer, G. D., R. J. Lavenberg, and G. E. McGowan. 1981. Abundance and vertical distribution of fish eggs and larvae in the southern California bight: June and October 1978. Rapports et Procès-Verbaux des Réunions Commission Internationale pour l'Exploration Scientifique de la Mer 178:165–168.

Carriker, M. R. 1951. Ecological observation on the distribution of oyster larvae in New Jersey estuaries. Ecological Monographs 21:19–38.

Creutzberg, F. 1961. The orientation of migrating elvers (*Anguilla anguilla* Turt.) in a tidal area. Netherlands Journal of Sea Research 1:257–338.

Creutzberg, F., A. T. G. W. Eltink, and G. J. Van Noort. 1978. The migration of plaice larvae, *Pleuronectes platessa*, into the western Wadden Sea. Pages 243–251 *in* D. S. McLusky and A. J. Berry, editors. Physiology and behavior of marine organisms. Pergamon, New York.

Crisp, D. J. 1974. Factors influencing the settlement of marine invertebrate larvae. Pages 177–265 *in* P. T. Grant and A. M. Mackie, editors. Chemoreception in marine organisms. Academic Press, New York.

Cronin, T. W., and R. B. Forward, Jr. 1979. Tidal vertical migration; and endogenous rhythm in estuarine crab larvae. Science (Washington, D.C.) 205:1020–1022.

Cronin, T. W., and R. B. Forward, Jr. 1983. Vertical migration rhythms of newly hatched larvae of the estuarine crab, *Rhithropanopeus harrisii*. Biological Bulletin (Woods Hole) 165:139–153.

Davis, R. 1962. Daily rhythm in the reaction of fish to light. Science (Washington, D.C.) 137:430–432.

de Bras, Y. M. 1979. Circadian rhythm in brain catecholamine concentrations in the teleost *Anguilla anguilla* L. Comparative Biochemistry and Physiology C, Comparative Pharmacology 62:115–117.

Emery, A. R. 1972. Eddy formation from an oceanic island: ecological effects. Caribbean Journal of Science 12:121–128.

Emery, K. O. 1967. Estuaries and lagoons in relation to continental shelves. American Association for the Advancement of Science Publication 83:9–11.

Enright, J. T. 1965. Entrainment of tidal rhythm. Science (Washington, D.C.) 147:864–867.

Enright, J. T. 1975. Orientation in time: endogenous clocks. Pages 917–944 *in* O. Kinne, editor. Marine ecology, volume 2, part 2. Wiley, New York.

Finger, T. E. 1976. An asymmetric optomotor response in developing flounder larvae (*Pseudopleuronectes americanus*). Vision Research 16:395–403.

Fluchter, J. 1965. Versuche zur Brutaufzucht der Seczunge *Solea solea* in kleinen Aquarien. Helgolaender Wissenschaftliche Meeresuntersuchungen 12:395–403.

Fore, P. L., and K. N. Baxter. 1972. Diel fluctuations in the catch of larval menhaden *Brevoortia patronus* at Galveston entrance, Texas. Transactions of the American Fisheries Society 101:729–732.

Fortier, L., and W. C. Leggett. 1982. Fickian transport and the dispersal of fish larvae in estuaries. Canadian Journal of Fisheries and Aquatic Sciences 39:1150–1163.

Fortier, L., and W. C. Leggett. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Canadian Journal of Fisheries and Aquatic Sciences 40:1543–1555.

Fukuhara, O. 1985. Functional morphology and behavior of early life stages of red sea bream. Bulletin of the Japanese Society of Scientific Fisheries 51:731–743.

Gardner, M. B. 1981. Effects of turbidity on feeding rates and selectivity of bluegills. Transactions of the American Fisheries Society 110:446–450.

Gibson, R. N. 1965. Tidal rhythmic activity in littoral fish. Nature (London) 207:544–545.

Gibson, R. N. 1971. Factors affecting the rhythmic activity of *Blennius pholis* (Teleostei). Animal Behaviour 19:336–343.

Gibson, R. N. 1978. Lunar and tidal rhythms in fish. Pages 201–214 *in* J. E. Thorpe, editor. The rhythmic activity of fishes. Academic Press, New York.

Gibson, R. N., J. H. S. Blaxter, and S. J. deGroot. 1978. Developmental changes in the activity rhythms of the plaice *Pleuronectes platessa*, L. Pages 169–186 *in* J. E. Thorpe, editor. The rhythmic activity of fishes. Academic Press, New York.

Haedrich, R. L. 1983. Estuarine fishes. Ecosystems of the World 26:183–207.

Harrison, W., J. J. Norcross, N. A. Pore, and E. M. Stanley. 1967. Circulation of shelf waters off the Chesapeake Bight. U. S. Department of Commerce, Environmental Science Services Administration Professional Paper 3, Washington, D.C.

Hasler, A. D., A. T. Scholz, and R. M. Horrall. 1978. Olfactory imprinting and homing in salmon. American Scientist 66:347–355.

Hempel, G. 1979. Early life history of marine fish. The egg stage. University of Washington, Washington Sea Grant Program, Seattle.

Hewitt, R. 1981. Eddies and speciation in the California Current. California Cooperative Oceanic Fisheries Investigations Report 22:96–98.

Hoar, W. S. 1951. The behavior of chum, pink, and coho salmon in relation to their seaward migration. Journal of the Fisheries Research Board of Canada 8:241–263.

Hoar, W. S. 1953. Control and timing of fish migration. Biological Reviews of the Cambridge Philosophical Society 28:437–452.

Hoar, W. S. 1958. Evolution of migratory behavior. Journal of the Fisheries Research Board of Canada 15:391–428.

Hubbs, C. L. 1958. *Dikellorhynchus* and *Kanazawaichthys:* nominal fish genera interpreted as based on prejuveniles of *Malacanthus* and *Antennarius*, respectively. Copeia 1958:282–285.

Hughes, D. A. 1969. Responses to salinity change as a tidal transport mechanism of pink shrimp *Penaeus duorarum*. Biological Bulletin (Woods Hole) 136: 43–53.

Hughes, D. A. 1972. On the endogenous control of tide associated displacements of pink shrimp, *Penaeus duorarum* Burkenroad. Biological Bulletin (Woods Hole) 142:271–280.

Hunter, J. R. 1967. Color changes of pelagic prejuvenile goatfish, *Pseudupeneus grandisquamis*, after confinement in a shipboard aquarium. Copeia 1967:850–852.

Hunter, J. R., and C. Sanchez. 1976. Diel changes in swimbladder inflation of the larvae of the northern anchovy, (*Engraulis mordax*). U.S. National Marine Fisheries Service Fishery Bulletin 74:847–855.

Hunter, J. R., and G. L. Thomas. 1974. Effect of prey distribution and density on the searching and feeding behavior of larval anchovy (*Engraulis mordax*) Girard. Pages 559–574 *in* J. H. S. Blaxter, editor. The early life history of fish. Springer-Verlag, New York.

Huyer, A., R. D. Pillsbury, and R. L. Smith. 1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnology and Oceanography 20:90–95.

Iwai, T. 1967. Structure and development of lateral line cupulae in teleost larvae. Pages 27–44 *in* P. H. Cahn, editor. Lateral line detectors. Indiana University Press, Bloomington.

Jellyman, D. J. 1979. Upstream migration of glass-eels (*Anguilla* spp.) in the Waikato River. New Zealand Journal of Marine and Freshwater Research 13:13–22.

Johnson, G. E., and J. J. Gonor. 1982. The tidal exchange of *Callianassa californiensis* (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon. Estuarine, Coastal and Shelf Science 14:501–516.

Kawamura, G., and S. Hara. 1980. The optomotor reaction of milkfish larvae and juveniles. Bulletin of the Japanese Society of Scientific Fisheries 46:929–932.

Kawamura, G., and K. Ishida. 1985. Changes in the sense organ morphology and behavior with growth in the flounder *Paralichthys olivaceus*. Bulletin of the Japanese Society of Scientific Fisheries 51:155–165.

Kendall, A. W., Jr., E. H. Ahlstrom, and H. G. Moser. 1984. Early life history stages of fishes and their characters. American Society of Ichthyologists and Herpetologists Special Publication 1:11–22.

Kendall, A. W., Jr., and N. A. Naplin. 1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. U.S. National Marine Fisheries Service Fishery Bulletin 79:705–727.

Kendall, A. W., Jr., and J. W. Reintjes. 1975. Geographic and hydrographic distribution of Atlantic menhaden eggs and larvae along the middle Atlantic coast from RV *Dolphin* cruises, 1965–66. U.S. National Marine Fisheries Service Fishery Bulletin 73:317–335.

Kingsford, M. J., and J. H. Choate. 1986. Influence of surface slicks on the distribution and onshore movement of small fish. Marine Biology (Berlin) 91:161–172.

Krygier, E. E., and W. G. Pearcy. 1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. U.S. National Marine Fisheries Service Fishery Bulletin 84:119–132.

Loeb, V. J. 1979. Vertical distribution and development of larval fishes in the north Pacific central gyre during summer. U.S. National Marine Fisheries Service Fishery Bulletin 77:777–793.

Marliave, J. B. 1977. Substratum preferences of settling larvae of marine fishes reared in the laboratory. Journal of Experimental Marine Biology and Ecology 27:47–60.

Marliave, J. B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. Transactions of the American Fisheries Society 115:149–154.

Matty, A. J. 1978. Pineal and some pituitary hormone rhythms in fish. Pages 21–30 *in* J. E. Thorpe, editor. The rhythmic activity of fishes. Academic Press, New York.

McCleave, J. D., and R. C. Kleckner. 1982. Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). Journal du Conseil, Conseil International pour l'Exploration de la Mer 40:262–271.

McCleave, J. D., and J. H. Power. 1978. Influence of weak electric and magnetic fields on turning behavior in elvers of American eel *Anguilla rostrata*. Marine Biology (Berlin) 46:29–34.

McHugh, J. L. 1967. Estuarine nekton. American Association for the Advancement of Science Publication 83:581–620.

Miles, S. G. 1968. Rheotaxis of elvers of the American eel *Anguilla rostrata* in the laboratory to water from different streams in Nova Scotia. Journal of the Fisheries Research Board of Canada 25:1591–1602.

Miller, J. M., J. P. Reed, and L. J. Pietrafesa. 1984. Patterns, mechanisms, and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. Pages 209–225 *in* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, editors. Mechanisms of migration in fishes. Plenum, New York.

Moore, J. W., and I. A. Moore, 1976. The basis of food selection in flounders, *Platichthys flesus* (L.) in the Severn estuary. Journal of Fish Biology 9:139–156.

Moser, H. G. 1981. Morphological and functional aspects of marine fish larvae. Pages 89–131 *in* R. Lasker, editor. Marine fish larvae: morphology, ecology, and relation to fisheries. University of Washington Press, Seattle.

Mundy, B. C. 1984. Yearly variation in the abundance and distribution of fish larvae in the coastal upwelling zone off Yaquina Head, Oregon, from June 1969 to August 1972. Master's thesis. Oregon State University, Corvallis.

Nelson, W. R., M. C. Ingham, and W. E. Schaff. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Fishery Bulletin 75:23–41.

Nordeng, H. 1977. A pheromone hypothesis for homeward migration in anadromous salmonids. Oikos 28:155–159.

Norris, K. S. 1963. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecological Monographs 33:23–62.

O'Connor, J. M. 1972. Tidal activity rhythm in the hogchoker, *Trinectes maculatus* (Bloch and Schneider). Journal of Experimental Marine Biology and Ecology 9:173–177.

Olla, B. L., and W. Marchoni. 1968. Rhythmic movements of cones in the retina of bluefish, *Pomatomus saltatrix*, held in constant darkness. Biological Bulletin (Woods Hole) 135:530–536.

Olla, B. L., A. L. Studholme, A. J. Bejda, and C. Samet. 1980. Role of temperature in triggering migratory behavior of the adult tautog *Tautoga onitis* under laboratory conditions. Marine Biology (Berlin) 59:23–30.

Owen, R. W. 1981. Fronts and eddies in the sea: mechanisms, interactions, and biological effects. Pages 197–233 *in* A. R. Longhurst, editor. Analysis of marine ecosystems. Academic Press, New York.

Ozsoy, E., and U. Unluata. 1982. Ebb-tidal flow characteristics near inlets. Estuarine, Coastal and Shelf Science 14:251–263.

Palmer, J. D. 1973. Tidal rhythms: the clock control of the rhythmic physiology of marine organisms. Biological Reviews of the Cambridge Philosophical Society 48:377–418.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biological Oceanography 1:175–203.

Pearcy, W. G., M. J. Hosie, and S. L. Richardson. 1977. Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus;* rex sole, *Glyptocephalus zachirus;* and petrale sole, *Eopsetta jordani*, in waters off Oregon. U.S. National Marine Fisheries Service Fishery Bulletin 75:173–184.

Pearcy, W. G., and S. S. Myers. 1974. Larval fishes of Yaquina Bay, Oregon; a nursery ground for marine fishes? U.S. National Marine Fisheries Service Fishery Bulletin 72:201–213.

Peterson, W. T., C. B. Miller, and A. Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Research, Part A, Oceanographic Research Papers 26: 467–494.

Pfeiler, E. 1984. Inshore migration, seasonal distribution and sizes of larval bonefish, *Albula*, in the Gulf of California. Environmental Biology of Fishes 10:117–122.

Pollock, B. R., H. Weng, and R. M. Morton. 1983. The seasonal occurrence of postlarval stages of yellow fin bream, *Acanthopagrus australis* (Gunther), and some factors affecting their movement into an estuary. Journal of Fish Biology 22:409–415.

Powles, H. 1981. Distribution and movements of neustonic young estuarine dependent (*Mugil* spp,. *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapports et Procès-Verbaux des Réunions Commission Internationale pour l'Exploration Scientifique de la Mer 178:207–210.

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. U. S. National Marine Fisheries Service Fishery Bulletin 75:125–145.

Rijnsdorp, A. D., M. van Stralen, and H. W. van der Veer. 1985. Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. Transactions of the American Fisheries Society 114:461–470.

Roessler, M. A., and R. G. Rehrer. 1971. Relation of catches of postlarval pink shrimp in Everglades National Park, Florida, to commercial catches on the Tortugas grounds. Bulletin of Marine Science 21:791–805.

Rogers, H. M. 1940. Occurrence and retention of plankton within the estuary. Journal of the Fisheries Research Board of Canada 5:164–171.

Rogers, S. G., T. E. Targett, and S. B. Van Sant. 1984. Fish-nursery use in Georgia salt-marsh estuaries: the influence of springtime freshwater conditions. Transactions of the American Fisheries Society 113:595–606.

Rosenberg, A. A. 1982. Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery areas. U.S. National Marine Fisheries Service Fishery Bulletin 80:245–252.

Rothlisberg, P. C., J. A. Church, and A. M. G. Forbes. 1983. Modelling the advection of vertically migrating shrimp larvae. Journal of Marine Research 41:511–538.

Sale, P. F. 1969. A suggested mechanism for habitat selection by the juvenile manini, *Acanthurus triostegus sandvicensis* Streets. Behaviour 35: 27–44.

Sale, P. F. 1970. Distribution of larval Acanthuridae off Hawaii. Copeia 1970:765–766.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series 13:311–315.

Shanks, A. L. 1985. Behavioral basis of internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. Marine Ecology Progress Series 24:289–295.

Shenker, J. M. 1985. Biology of neustonic larval and juvenile fishes and crabs off Oregon, 1984. Doctoral dissertation. Oregon State University, Corvallis.

Shenker, J. M., and J. M. Dean. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity, and temporal variation. Estuaries 2:154–163.

Staples, D. J. 1980. Ecology of juvenile and adolescent banana prawns, *Penaeus merguiensis*, in a mangrove estuary and adjacent off-shore area of the Gulf of Carpenteria. Australian Journal of Marine Freshwater Research 31:635–652.

Tanaka, M. 1985. Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream *Pagrus major* to a nursery ground. Transactions of the American Fisheries Society 114: 471–477.

Thorpe, J. E., editor. 1978. The rhythmic activity of fishes. Academic Press, New York.

Tsuruta, Y. 1978. Field observations on the immigration of larval stone flounder into the nursery ground. Tohoku Journal of Agricultural Research 29(3–4): 136–145.

Tzeng, W. N. 1985. Immigration timing and activity rhythms of the eel, *Anguilla japonica*, elvers in the estuary of northern Taiwan, with emphasis on environmental influences. Bulletin of the Japanese Society of Fisheries Oceanography 47–48:11–28.

Venema, S. C., and F. Creutzberg. 1973. Seasonal migration of the swimming crab *Macropipus holsatus* in an estuarine area controlled by tidal streams. Netherlands Journal of Sea Research 7:94–102.

Victor, B. C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Canadian Journal of Fisheries and Aquatic Sciences 43:1208–1213.

Weihs, D. 1978. Tidal stream transport as an efficient method for migration. Journal du Conseil, Conseil International pour l'Exploration de la Mer 38: 92–99.

Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 77:339–358.

Weinstein, M. P. 1983. Population dynamics of an estuarine-dependent fish, the spot (*Leiostomus xanthurus*), along a tidal creek–seagrass meadow coenocline. Canadian Journal of Fisheries and Aquatic Sciences 40:1633–1638.

Weinstein, M. P., S. L. Weiss, R. G. Hodson, and L. R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. U.S. National Marine Fisheries Service Fishery Bulletin 78:419–436.

Williams, A. B., and E. E. Deubler. 1968. A ten year study of meroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Science 9:27–41.

Wroblewski, J. S. 1982. Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. Deep-Sea Research 29:665–686.

Yamashita, Y., D. Kitagawa, and T. Aoyama. 1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel, *Ammodytes personatus*. Bulletin of the Japanese Society of Scientific Fisheries 51:1–5.

Yoklavich, M. 1982. Growth, food consumption, and conversion efficiency of juvenile English sole (*Parophrys vetulus*). Pages 97–105 *in* G. M. Cailliet and C. A. Simenstad, editors. Gutshop 81, fish food habits studies. University of Washington, Washington Sea Grant Program, Seattle.

# PELAGIC BIOGEOGRAPHY OF THE ARMORHEAD, *PSEUDOPENTACEROS WHEELERI*, AND RECRUITMENT TO ISOLATED SEAMOUNTS IN THE NORTH PACIFIC OCEAN

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## ABSTRACT

The pelagic armorhead, *Pseudopentaceros wheeleri*, occurs widely in the North Pacific Ocean. Benthic specimens have been taken from Japan, the Hawaiian Archipelago, and the west coast of North America, but the main reproductive populations are located on southern Emperor-northern Hawaiian Ridge seamounts between lat. 29° and 35°N. The period between spawning and recruitment to the seamounts is apparently between 1.5 and 2.5 years, suggesting an extended pelagic existence. We describe the distributional patterns in the North Pacific based upon over 30 years of published and unpublished records. The majority of pelagic specimens are captured in the subarctic water mass in the northeast Pacific. Based upon the distributional patterns and the oceanography of the North Pacific, we propose migratory paths for both the main population and for the individuals that occur rarely in other locations. The long pelagic period and variability in ocean conditions may play an important role in recruitment to seamounts and the variability in year-class strength for this species.

The pelagic armorhead, *Pseudopentaceros wheeleri*, is a member of the boarfish family Pentacerotidae. Until recently, considerable confusion existed about its taxonomy and distribution. Originally described as *Pentaceros richardsoni* Smith 1844, it was thought to be distributed virtually worldwide, with centers of abundance in the North Pacific and in the South Atlantic near South Africa (Fujii 1986). Occurrences were typically sporadic; most records were from pelagic captures, hence the name pelagic armorhead. Several authors, including Welander et al. (1957), Clemens and Wilby (1961), and Wagner and Bond (1961), used the name *Pseudopentaceros richardsoni*, but more recent studies used the original binomial following Follett and Dempster (1963).

The 1967 discovery of large concentrations of armorhead in the mid-Pacific, over southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts (from lat. 29° to 35°N) (Sasaki 1974; Uchida and Tagami 1984) stimulated increased interest in this species. Over the next 10 years, nearly 1 million metric tons (t) were taken by Soviet and Japanese trawlers (Borets 1975; Takahashi and Sasaki 1977). The increased availability of specimens allowed Hardy (1983) to revise the family. He first separated the *Pentaceros richardsoni* complex from other members of the genus by referring it to *Pseudopentaceros* Bleeker, based on morphological considerations. Second, he separated the complex into three species: *P. richardsoni* confined to the Southern Hemisphere, and *P. wheeleri* and *P. pectoralis* in the North Pacific. The features used to distinguish *P. wheeleri* and *P. pectoralis* were largely morphological. *Pseudopentaceros pectoralis* is more robust and deeper bodied and its distribution is typically pelagic; *P. wheeleri* was known only from benthic specimens on seamounts. Hardy (1983), however, lacked transitional specimens; subsequent work based on morphological and electrophoretic grounds revealed that *P. wheeleri* was a morphological derivative of *P. pectoralis*, with changes occurring after settlement. The deeper bodied pelagic form ceases growth in length after recruiting to the seamounts and instead transforms body shape to a leaner form. "Fat" and "lean" specimens of the same length thus differ significantly in appearance (Humphreys et al. in press).

*Pseudopentaceros wheeleri* has an unusual life history. Spawning occurs at the benthic population centers at the SE-NHR seamounts between November and March (Sasaki 1974; Borets 1976; Bilim et al. 1978). Larvae and juveniles are pelagic (Honma and Mizusawa 1969; Fedosova and Komrokov 1975; Borets and Sokolovsky 1978) and widely distributed in the North Pacific. Recruitment to the seamounts

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occurs between ages 1.5 and 2.5 years, but in the major spawning population centers, over 95% of the fish are <2 years (Uchiyama and Sampaga[3]). This lack of older specimens and presence of fish in poor physiological condition has led to suggestions that this species is semelparous, with death after a single spawning (Humphreys and Tagami 1986; Humphreys et al. in press). The long interval between spawning and recruitment for this species suggests that oceanographic conditions in the North Pacific regulate its distribution (Boehlert 1986).

Published records of the pelagic distribution of *P. wheeleri* are too few and varied to understand its biogeography. In different years, specimens have been caught in the Gulf of Alaska, near the Aleutian Islands, and off the coasts of Japan, Oregon, California, and British Columbia. In this paper, we document the pelagic and benthic occurrences from both published and unpublished accounts, consider this distributional pattern in light of general oceanographic conditions in the North Pacific, propose hypotheses about the migration and recruitment of armorhead to the seamounts of the central North Pacific, and assess interannual variation in abundance and how it may relate to oceanographic variability.

## MATERIALS

The data sources used include published and unpublished collection records from throughout the North Pacific Ocean. Published records on occurrences in Japan (Abe 1957, 1969; Zama et al. 1977; Okamura et al. 1982), the eastern North Pacific (Welander et al. 1957; Larkins 1964; Honma and Mizusawa 1969; Chikuni 1970; Ignell et al. 1986), and the west coast of North America (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965) were typically of single or a few specimens. Larger numbers of unpublished collection records were in data from large-scale surveys (Table 1). These data

TABLE 1.—Data bases searched for pelagic armorhead, *Pseudopentaceros wheeleri*, captures excluding single collections and literature reports. Areas and seasons are averages over the years covered.

| Data source | Years, season effective | Area | |
|---|---|---|---|
| | | Lat. N | Long. |
| Salmon drift gill-net surveys[1] | 1972–86, spring-fall | 38°–65° | 140°E–166°W |
| University of Washington (FRI) purse seining, longlining[2] | 1956–82, spring-summer | 42°–60° | 165°E–125°W |
| Canada salmon longlining[2] | 1962–67, spring-summer | 42°–54° | 120°–145°W |
| Bureau of Commercial Fisheries salmon gill net[2,3] | 1955–71, spring-summer | 40°–60° | 165°E–125°W |
| *Oshoro Maru* salmon gill-net-longline surveys[4] | 1963–66, 1968, 1969, 1971, 1974–86, spring-summer | 36°–66° | 163°E–124°W |
| *Hokusei Maru* squid and salmon gill-net surveys[4] | 1973–86, summer | 18°–58° | 141°E–156°W |
| Japan Marine Fishery Resource Research Center pomfret surveys[5] | 1979–82, all months | 22°–49° | 143°E–124°W |
| Japanese commercial whaling reports[6] | 1952–79, summer | 40°–58° | |
| Pacific Biological Station gill-net surveys[7] | 1983, 1985–86, spring-summer | 47°–54° | 138°–130°W |
| Taiwan Fisheries Research Institute squid surveys[8] | 1986, July-August | 38°–46° | 153°E–175°W |
| National Marine Fisheries Service Auke Bay cooperative squid gill-net surveys[9] | 1985–86 | 43°–55° | 145°–175°W |
| Japan Fisheries Agency squid gill-net surveys | 1986–87, July-August | 36°–47° | 150°–165°W |

[1] Salmon research data file, North Pacific Ocean, 1972–86. Salmon Division, Far Seas Fisheries Research Laboratory, Shimizu, Japan.

[2] Macy et al. 1978.

[3] Larkins 1964.

[4] Data record of oceanographic observations and exploratory fishing. No. 1 (1957)–No. 28 (1985). Faculty of Fisheries, Hokkaido University.

[5] Japan Marine Fishery Resourse Research Center 1980, 1983a, 1983b, 1985.

[6] Biological data file of whales in the North Pacific Ocean, 1952–79. Whale Section, Far Seas Fisheries Research Laboratory, Shimizu, Japan. See also Chikuni (1970).

[7] Sloan 1983; Robinson and Jamieson 1984.

[8] Z. Shyu, Taiwan Fisheries Research Institute, Keelung 20220, Taiwan, pers. commun. May 1987.

[9] Ignell et al. 1986.

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[3] Uchiyama, J. H., and J. Sampaga. In review. Age and growth of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Hancock Seamounts. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

are seasonally limited to primarily spring, summer, and early fall months, but cover 1952–87 and provide broad geographic coverage between lat. 18° and 66°N. Greater detail and a summary of many of these surveys are provided by Macy et al. (1978). Since armorhead were an incidental catch, it is difficult to assess the relative value of the different surveys with respect to sampling effort.

The most typical sampling gears used were longlines, gill nets, and purse seines targeting salmon, squid, or pomfret; rarer collections were made with plankton nets, dip nets, or hook and line. Thus, sampling was typically in surface waters, most likely in the upper 50 m; the true depth distribution of the pelagic animals, however, is unknown. The only other "gear" was the sei whale, *Balaenoptera borealis*, from which stomach contents were studied for about 27 years; Chikuni (1970) reported armorhead in the stomachs.

## RESULTS AND DISCUSSION

### Distributional Patterns

The known center of distribution and spawning for benthic *P. wheeleri* is in the SE-NHR seamount region, bounded by lat. 29°–35°N and long. 171°E–179°W (Takahashi and Sasaki 1977; Humphreys and Tagami 1986). These reproductive fish are typically between 23.0 and 28.5 standard length (SL) (Sasaki 1986) and range in age from 1.5 to 2.5 years (Uchiyama and Sampaga fn. 3). They are found at depths between 200 and 500 m (Takahashi and Sasaki 1977). Other benthic occurrences have been recorded but are sporadic (Fig. 1). Several specimens were captured off Japan in 1957 (Abe 1957), 1969, 1971–73, 1976 (Zama et al. 1977), and 1979 (Okamura et al. 1982). These fish were typically the same size as those captured on the seamounts, but no mention of reproductive status was made. Fish of similar length occur rarely on the west coast of North America, but only between lat. 37°00′ and 44°25′N (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965). Again, reproductive status is unknown for these specimens. No benthic occurrences off British Columbia or Alaska have been reported, despite extensive trawling surveys which included seamounts (Hughes 1981; Alton 1986). Large specimens have been taken rarely in the Hawaiian Archipelago (Fig. 1; Randall 1980; Humphreys et al. in press) and are typically 4–5 years old and appear to be in reproductive condi-

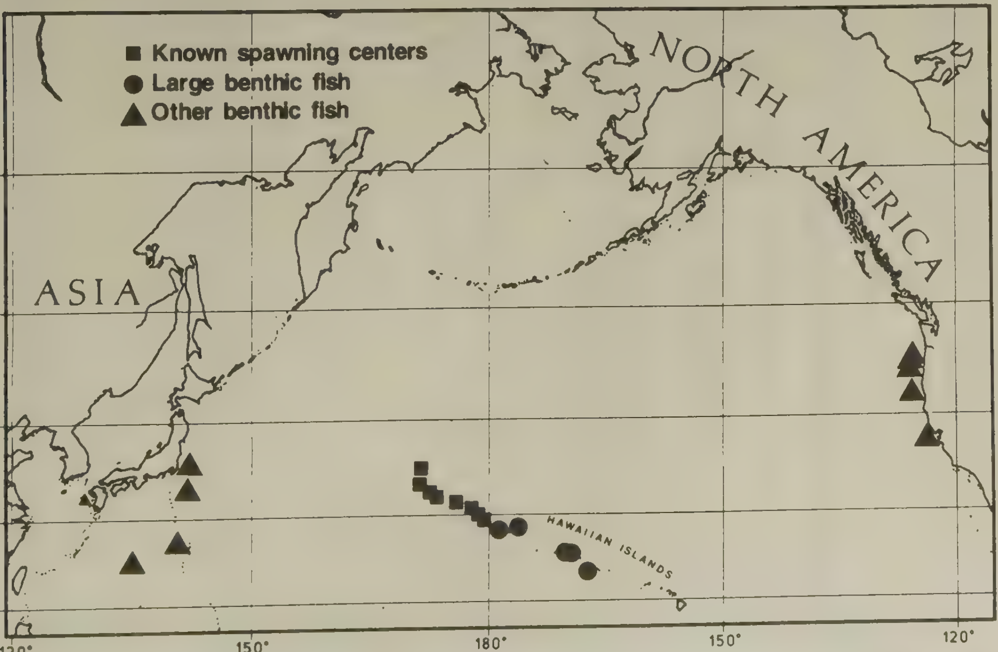

FIGURE 1.—Known distribution of benthic occurrences of pelagic armorhead, *Pseudopentaceros wheeleri*. Squares represent the main population centers at central North Pacific seamounts. All others are rare or sporadic occurrences.

tion. Their relationship with the SE-NHR seamount populations is unknown.

The most common pelagic occurrences (1955–87) were fish ranging from 18 to 26 cm SL; smaller sizes are poorly represented, probably because of the nature of the sampling gear. Smaller specimens were generally captured with plankton nets (Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), dip nets (Honma and Mizusawa 1969; Randall 1980; Fujii[4]), and in one case, in a whale stomach (Kawamura 1982). The sea-surface temperatures at which the specimens were captured ranged from 8.6° to 15.0°C (average 12.1°C). For all years, pelagic captures were restricted to the eastern North Pacific, with the exceptions of larvae or early juveniles captured near the spawning centers at the seamounts (Komrakov 1970; Table 2), over 20 specimens in a Bryde's whale stomach in 1979 (Kato[5], Fig. 2B), and two individuals captured in 1986 at long. 155°E (Fig. 2). This is despite extensive sampling in the western North Pacific, particularly by the Japan Marine Fishery Resource Research Center (JAMARC) and the Hokkaido University, and in the Bering or Okhotsk Seas (Table 1).

Pelagic captures in the 1950's were sporadic, but several fish were taken north of lat. 50°N, especially in 1958 (Fig. 2A). Relatively few were captured in the 1960's, with the exception of July through early August 1969, when the armorhead was an impor-

TABLE 2.—Pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, for which sizes were available. The growth curve from Uchiyama and Sampaga (text footnote 3), based upon enumeration of daily growth increments, was used to deduce age from length. For the youngest fish (bottom), average readings from daily growth increments, rather than the growth curve, were used. Data are from various published sources and collections listed in Table 1. (SST = sea-surface temperature.)

| Year | Date | Lat. N | Long. | SST | Standard length (mm) | Age (yr) | No. | Gear |
|---|---|---|---|---|---|---|---|---|
| 1955 | 9/27 | 45°41′ | 165°5′W | — | 108–122 | 0.38–0.42 | 2 | Gill net |
| 1955 | 9/27 | 45°35′ | 165°5′W | — | 200 | 0.79 | 1 | Dip net |
| 1956 | 7/31 | 45°49′ | 160°3′W | 12.2 | 245 | 1.29 | 1 | Gill net |
| 1956 | 9/15 | 45°00′ | 155°00′W | 12.1 | 245 | 1.29 | 2 | Gill net |
| 1956 | 9/17 | 49°00′ | 150°00′W | 13.2 | 245 | 1.29 | 1 | Gill net |
| 1956 | 9/17 | 51°00′ | 150°00′W | 11.0 | 245 | 1.29 | 1 | Gill net |
| 1958 | 8/14 | 44°39′ | 174°48′W | — | 64–91 | 0.26–0.33 | 2 | Dip net |
| 1958 | 8/25 | 49°43′ | 146°10′W | 11.8 | 256 | 1.50 | 1 | Gill net |
| 1963 | 8/24 | 49°0′ | 162°0′W | 12.9 | 249 | 1.40 | 1 | Gill net |
| 1967 | 6/15 | 54°38′ | 150°1′W | 8.8 | 121–134 | 0.42–0.46 | 4 | Dip net |
| 1968 | 7/ | 41°30′ | 165°30′W | — | 285 | >2.00 | 1 | Handline |
| 1969 | 4/1 | 29°48′ | 179°5′E | — | 8–23 | 0.08–0.25 | ? | Plankton |
| 1969 | 4/1 | 31°6′ | 176°0′E | — | 8–23 | 0.08–0.25 | — | Plankton |
| 1969 | 4/1 | 32°6′ | 173°0′E | — | 8–23 | 0.08–0.25 | — | Plankton |
| 1972 | 5/21 | 38°30′ | 175°3′W | 14.3 | 42–50 | 0.21–0.23 | 5 | Whale stomach |
| 1984 | 7/25 | 45°30′ | 155°0′W | 13.0 | 262–265 | 1.81–2.02 | 3 | Gill net |
| 1984 | 7/25 | 45°26′ | 154°58′W | 12.0 | 278 | >2.00 | 2 | Longline |
| 1985 | 7/9 | 46°57′ | 129°4′W | — | 272 | >2.00 | 1 | Gill net |
| 1985 | 7/10 | 47°30′ | 128°36′W | — | 272–298 | >2.00 | 2 | Gill net |
| 1985 | 7/11 | 47°59′ | 129°19′W | — | 277 | >2.00 | 1 | Gill net |
| 1985 | 7/13 | 46°23′ | 131°29′W | — | 188–219 | 0.71–0.94 | 5 | Gill net |
| 1985 | 7/14 | 46°40′ | 131°8′W | — | 183–233 | 0.68–1.1 | 9 | Gill net |
| 1985 | 7/15 | 46°35′ | 131°5′W | — | 206 | 0.83 | 1 | Gill net |
| 1985 | 7/19 | 46°54′ | 131°28′W | — | 190–217 | 0.72–0.92 | 2 | Gill net |
| 1985 | 7/21 | 47°18′ | 130°23′W | — | 191–220 | 0.73–0.95 | 3 | Gill net |
| 1985 | 7/22 | 47°35′ | 130°48′W | — | 190–201 | 0.72–0.79 | 2 | Gill net |
| 1985 | 7/23 | 47°37′ | 130°31′W | — | 198–200 | 0.77–0.79 | 2 | Gill net |
| 1985 | 7/12 | 47°0′ | 155°1′W | 11.6 | 263–265 | 1.87–2.02 | 2 | Longline |
| 1985 | 7/13 | 45°28′ | 155°5′W | 11.8 | 238–262 | 1.17–1.81 | 12 | Longline |
| 1985 | 7/11 | 47°0′ | 155°0′W | 11.6 | 248–262 | 1.35–1.81 | 5 | Gill net |
| 1985 | 7/12 | 45°30′ | 155°0′W | 11.8 | 235–240 | 1.12–1.20 | 4 | Gill net |
| 1985 | 7/13 | 44°0′ | 155°0′W | 12.8 | 248–258 | 1.35–1.63 | 4 | Gill net |
| 1985 | 2/23 | 30°16′ | 181°18′W | — | 8–15 | 0.08–0.16 | 15 | Neuston |
| 1985 | 2/24 | 29°27′ | 180°56′W | — | 5–15 | 0.04–0.16 | 15 | Neuston |
| 1986 | 8/3 | 43°51′ | 164°54′W | 13.0 | 50–100 | 0.23–0.35 | 5 | Dip net |

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[4] E. Fujii, Nippon Luther Shingaku Daigaku, Tokyo, Japan, pers. commun. July 1987.

[5] H. Kato, Whales Research Institute, Tokyo, Japan, pers. commun. December 1987.

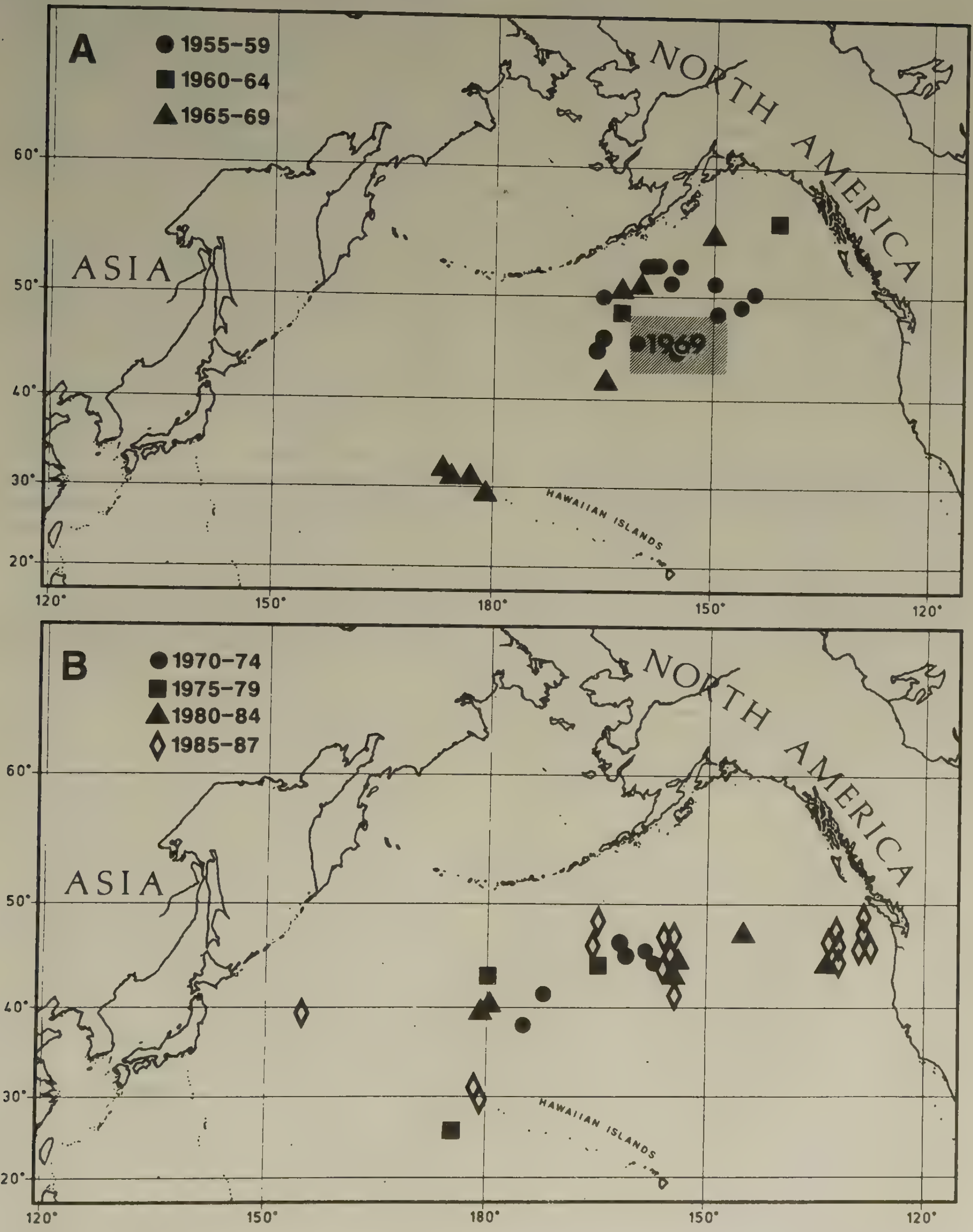
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FIGURE 2.—Records of pelagic occurrences of armorhead, *Pseudopentaceros wheeleri*, in the North Pacific. Most data were obtained from either published records or unpublished data described in Table 1: Each symbol represents a collection taking armorhead, rather than single specimens. (A) 1955–69. Here, note that the area in the box contains the locations of 195 sei whales captured in July–August 1969 that had fed extensively upon armorhead. The samples from the central Pacific were larvae and early juveniles (Fedosova and Komrakov 1975). (B) 1970–87.

tant diet component of sei whales taken by the Japanese commercial fleet. This species normally feeds on zooplankton and micronekton (Kawamura 1982), but in this year, 195 whales were recorded to have fed extensively on armorhead. Although data records for whale stomach contents extend from 1952 to 1979, 1969 was the only year when large numbers fed on armorhead, with the exception of two occurrences each in 1971 and 1972. Based on the known feeding mode of sei whales, Chikuni (1970) suggested that the armorhead apparently schools in surface waters. In the 1970's, catches were relatively small, but in the 1980's, specimens have been captured in each year, with the greatest catches in 1985. In that year, fish occurred in more easterly areas as compared to other years.

## Relationship of Distribution Patterns to North Pacific Oceanography

The SE-NHR seamounts are located in the mid-Pacific transition zone, between subarctic and subtropical water masses (Roden 1970). The spawning season of armorhead typically lasts from late November through March (Sasaki 1974; Bilim et al. 1978), and larvae are neustonic, at least through the first few months of life (G. W. Boehlert unpubl. data). Near surface drift in this region is largely wind driven (McNally 1981); as shown by Lagrangian drifters, mean surface flow in the SE-NHR seamount region during winter months is typically eastward (Kirwan et al. 1978; Emery et al. 1985) or southeastward (McNally et al. 1983), and long-term mean Ekman transport has a southeastward component (Favorite et al. 1976). Based on mean ship-drift data, progressive vector diagrams over a 3-mo period, with starting points at four SE-NHR seamounts (Bakun[6]), show this typical eastward flow with a southward component (Fig. 3). If pelagic armorhead followed such a pattern, individuals would remain in the subtropical gyre, continuing eastward and then turning south, entering the California Current system. The scarcity of specimens in this region (Figs. 1, 2) suggests instead that most fish move northeastward in some manner, entering subarctic waters and residing within the Alaska gyre; surface drift in winter is northeastward in anomalous years (McNally 1981), and average

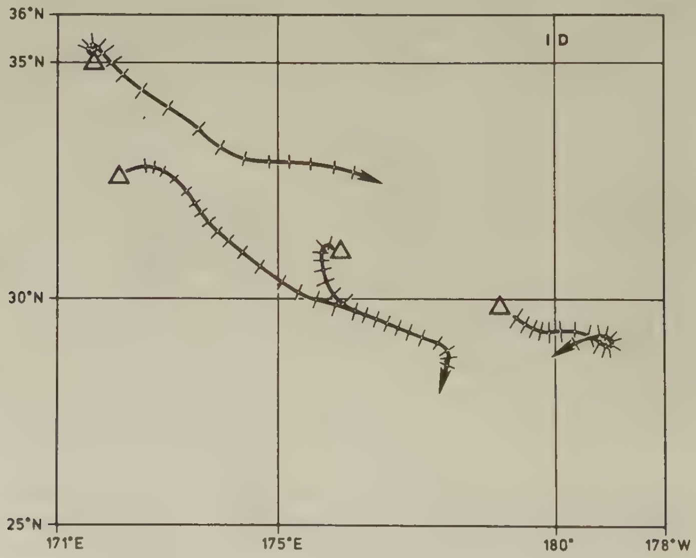

FIGURE 3.—Progressive vector diagrams of mean surface currents (starting date, 15 December; duration, 90 days), from long-term mean ship drift data from 1° squares, with distances calculated on a daily basis. Triangles indicate starting locations at four seamounts with armorhead spawning populations. Each mark on the vector between the origin and arrow represents a 5-d period. See text footnote 6.

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[6] Compilation by the NMFS Pacific Fisheries Environmental Group from historic ship drift files assembled by the U.S. Naval Oceanographic Office (A. Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942, pers. commun. April 1987.

surface flow is in this direction in summer months (McNally et al. 1983).

The two available studies on larval distribution of armorhead are conflicting and suggest that patterns of movement may differ from year to year. Komrakov (1970) conducted surveys in March–April 1969 and observed larvae only at northern seamounts and in the open ocean several hundred kilometers northeast of the SE-NHR seamounts. Borets (1979), however, observed 5–20 mm larvae remaining mostly around the seamounts, with highest abundance south of lat. 33°N in 1976. Because spawning occurs at seamounts northwest of this area, this pattern is consistent with southeastward drift during the first few months of life (Fig. 3). If larvae remain in the seamount region, they could be transported to the northeast in summer months, or they may actively migrate northeastward after reaching the juvenile stage. A similar migration apparently occurs for the pomfret, *Brama japonica*, which prior to spawning moves into the North Pacific current region in a broad latitudinal band between the subtropical convergence and the subarctic boundary; immature fish and spent adults then move northward into the subarctic region to feed during April–May (Shimazaki and Nakamura 1981). The pomfret differs from the armorhead, however, in that it remains pelagic throughout its life and also is abundant in the western North Pacific. Larval and juvenile *Brama* sp. do occur in the same area as larval armorhead (Borets and Sokolovsky 1978; G. W. Boehlert unpubl. data).

A possible scenario of movements after the larval stage can be deduced from the ages of individuals captured in different regions. Based upon the growth of pelagic armorhead (Uchiyama and Sampaga fn. 3), most of the larger specimens indicated in Figure 2 are from 1 to 2 years old, and the pelagic duration for this species is most often from 1.5 to 2.5 years. Using daily growth increments for larval and small juveniles and fitted growth curves for larger juveniles and adults, one can convert lengths to ages. The pelagic specimens of known length range in estimated age from 0.04 to >2 years (Table 2). The youngest animals are typically found in the region of the seamounts (Komrakov 1970; Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), but intermediate-sized fish are found north and east of the seamounts. Different age groups seem to be distributed in different areas in the eastern North Pacific (Fig. 4). Armorhead spawn in the seamount region (as area A in Figure 4) during November to March, and juveniles 5–25 mm long are found in the SE-NHR seamounts area from February to early April (Fedosova and Komrakov 1975; Borets 1979). Subsequent occurrences of fish older than 0.25 year (Table 2) are found only in the region northeast of the seamounts and in the Gulf of Alaska (area B in Figure 4). Northeastward movements are contrary to mean ocean currents, but Roden et al. (1982) described intense northward flow along the axis of the southern Emperor Seamounts that could conceivably play a role in transport of fish at the youngest stages.

Recruitment of later stage armorhead to the seamounts requires movement to the west. The only significant westward circulation in the North Pacific is found in the Alaskan Stream (Favorite 1967). This narrow current occurs north of lat. 51°N and extends westerly to near long. 170°E, where it splits to two branches, one turning northerly into the Bering Sea and the other southerly under the influence of the northern Emperor Seamounts or Kormandorskie Ridge (Favorite 1967; dashed line in Figure 4). Darnitsky et al. (1984) described southerly movement of this water to at least lat. 40°N and suggested that it played a role in transport of planktonic food for armorhead on the seamounts. Unless returning armorhead are deep in the water column and therefore not sampled, distributional data (Fig. 2) do not support this route for westerly movement. Fish near recruitment size and age are instead captured in the region marked C on Figure 4, south of the area where younger fish are captured. These fish apparently migrate back to the region of the seamounts by some unknown, but probably active, mechanism.

Two less important, but plausible, movement patterns may explain the rarer occurrences in southern Japan, off Oregon and California, and in the Hawaiian Archipelago (Fig. 4). Chelton (1984) discussed possible interannual changes in the latitudinal position of the West Wind Drift which may lead to differing magnitudes of transport in the Alaska and California Currents. The rare benthic occurrences of the pelagic armorhead off the west coast of North America (area D in Figure 4) may come from specimens that drift southward in the California Current in years of greater southern transport. Some of these may not settle out and remain within the subtropical gyre, possibly recruiting to the Hawaiian chain far to the south of the normal reproductive population. This route, because of its distance, apparently takes considerably longer than that in the subarctic gyre; based upon satellite drifters, McNally et al. (1983) suggested that a full circuit of the subtropical gyre takes 4.5 years. The armorhead collected in the Northwestern Hawaiian

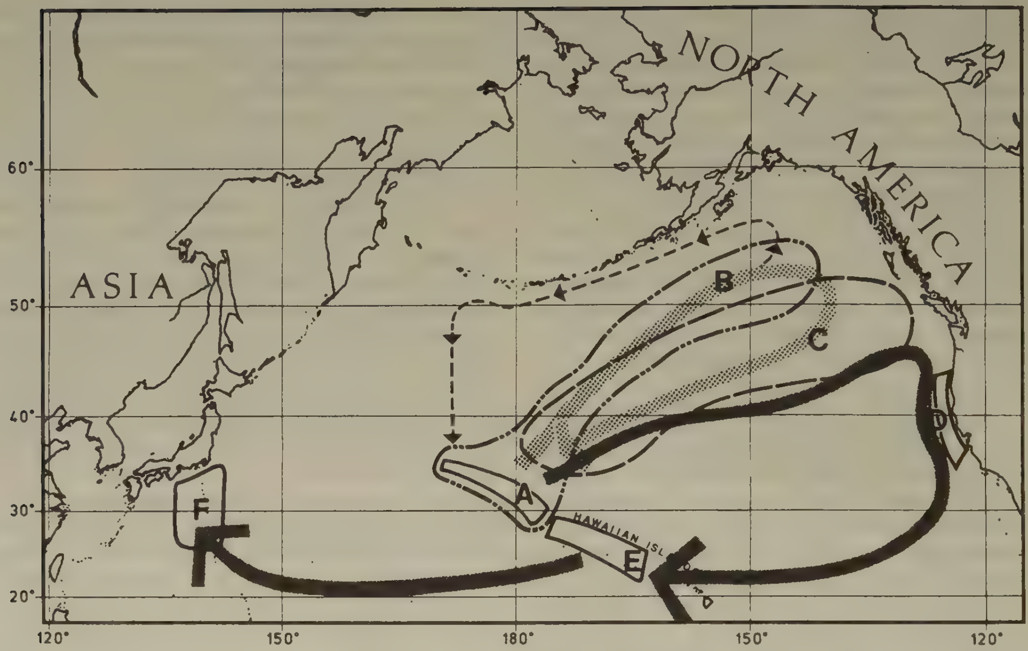

FIGURE 4.—Distributions of benthic and pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, by age group with possible patterns of movement. Area A represents the major spawning area, and area E the region inhabited by the large, older specimens. Area B is the region in which specimens younger than 1 year have been captured, and area C where fish from 1 to 2 years old have been captured. The arrow through this region represents the main population movement pattern. Other arrows represent possible movements for stray fish. Areas marked D and F represent locations of benthic collections from California and Japan, respectively.

Islands (area E in Figure 4) are typically larger than those in the normal part of the range and are correspondingly older, with ages estimated at 4 or 5 years (Humphreys et al. in press), similar to the time suggested for a circuit of the gyre by McNally et al. (1983).

The other plausible movement pattern can be used to explain the existence of specimens in Japan. Benthic specimens of armorhead are rarely captured in Japan (Fig. 1); a report of 3,000 t landed in 1969 by Soviet fishermen in this region (Abe 1969) may be in error, since the Soviet fishery on the SE-NHR seamounts developed heavily that year (Borets 1975) and SE-NHR fish were likely sold in Japan. The reproductive condition of these animals is not known, so the source of the spawning population supplying them is at question. The large, reproductive individuals in area E (Fig. 4) have been found as far south as lat. 23°43′N (Humphreys et al. in press). It is possible that larvae and juveniles are transported to Japan in the northern part of the North Equatorial Current (Uda and Hasunuma 1969). This is consistent with the capture of over 20 fish in a Bryde's whale stomach in September 1979 at lat. 26°N (H. Kato fn. 5; Fig. 2B). Subsequent captures of this species have not been made in Japanese waters, where their presence may require a rare recruitment event from an upstream population source, as has been suggested for seamount populations of lobsters (Lutjeharms and Heydorn 1981). These animals may also remain within a gyral circulation, however, as suggested by the presence of two specimens captured in the Kuroshio in 1986 (Fig. 2B).

## Recruitment to the Seamounts

The seasonal timing of the recruitment of the pelagic armorhead to the SE-NHR seamounts is unknown. That no records of larger pelagic fish captured near the seamounts (Fig. 2) exist may be an artifact of sampling in inappropriate seasons or lack of sampling in deeper water. The youngest benthic specimens from the seamounts were slightly in excess of 1.5 years in early summer (Uchiyama and Sampaga fn. 3) and 2 years in winter, suggesting that some recruitment occurs in spring.

In most fisheries, temporal recruitment patterns can be discerned from length-frequency analyses, because the smaller recruits represent a larger proportion of the population during the season of recruitment. For the armorhead, no increase in smaller size classes is apparent in monthly length-frequency samples. This may be due to cessation of somatic growth after recruitment to the seamount (Humphreys and Tagami 1986; Uchiyama and Sampaga fn. 3). Early recruits, with their deeper bodies and greater fat content, differ morphologically from longer seamount residents. The transition from so-called "fat" to "lean" morphotypes occurs in association with development of gonads (Humphreys et al. in press). Thus, an index of morphological change can be used to detect recruitment patterns, much the same as length frequencies can be used for other species. Condition factor is frequently used to assess "fatness" of fish; it is normally expressed as weight divided by length to a power (typically 3) multiplied by some scaling factor (Ricker 1975). For armorhead, there is a marked change in condition factor with morphological change; newly recruiting fish have high condition factors relative to intermediate or lean fish. By considering the monthly proportion of fish above an arbitrary value of condition factor, we can estimate the influx of new recruits to the seamounts. During May 1972–December 1973, the major influx of new recruits with a high condition factor occurred in April–May 1973 (Fig. 5). The data for 1972 are incomplete, but some recruitment apparently occurred in August and September (Fig. 5). Differences in seasonality of recruitment between 1972 and 1973 may be indicative of interannual variability in temporal recruitment patterns.

An influx of fish to the seamounts may also be reflected in the catch per unit effort (CPUE), an index of stock abundance. Monthly averages of CPUE (in metric tons per hour) by Japanese trawlers for armorhead at the SE-NHR seamounts were highest in March and April (Sasaki 1986). Overall armorhead CPUE decreased continuously from 54.1 t/h in 1972 to only 0.3 t/h in 1982 (Sasaki 1986) and further decreased to 0.06–0.07 t/h in 1983–85 (T. Sasaki unpubl. data). The estimated CPUE in 1986, however, was 0.31 t/h, an increase of four or five times that in the previous year. The CPUE of trawlers operating in May–September 1986 was highest in May, decreased in June and July, but increased slightly in August and Septem-

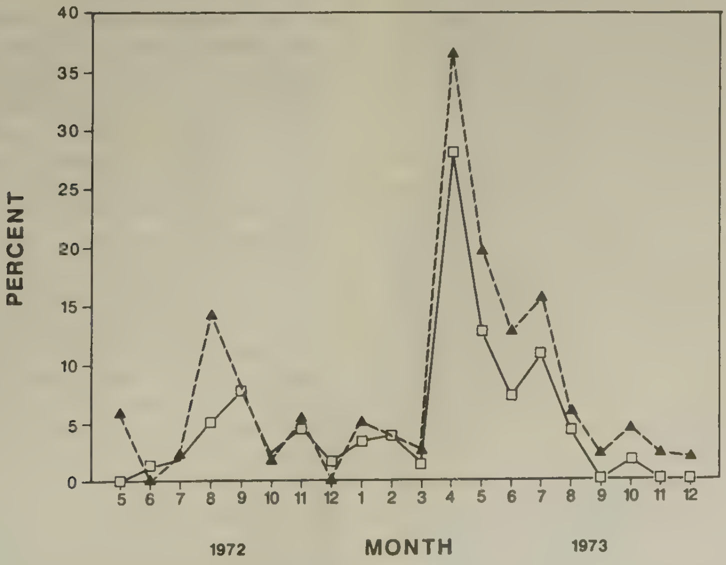

FIGURE 5.—Seasonality of the proportion of armorhead, *Pseudopentaceros wheeleri*, with condition factors ≥2.0 from four seamounts of the northern Hawaiian Ridge (Southeast Hancock, Northwest Hancock, C-H, and Colahan) for 1972–73. Squares, males; triangles, females. Data are based upon 2,104 males and 1,704 females.

ber. Based on all the information, the major recruitment may occur in spring with some additional recruitment in August and September (Fig. 5); data are not sufficient to determine the recruitment pattern in detail.

A broad geographic separation exists between the location of pelagic captures of larger armorhead and the location of the spawning populations (Figs. 2, 4). If recruitment to the seamounts occurs predominantly in spring (as suggested for 1973 in Figure 5), then temporal sampling patterns may have missed these fish, although JAMARC pomfret surveys covered this area in some seasons (Table 1). Locating the seamounts, which have small (2–5 km) summits must be a formidable task given the wide ocean areas over which armorhead are distributed. A similar situation exists for rock lobster, *Jasus tristani*, in the South Atlantic, that recruits from an upstream population some 2,000 km away and in sufficient numbers to support a fishery on Vema Seamount in some years (Lutjeharms and Heydorn 1981).

Open-ocean migrations of fishes may depend upon many potential cues, including electric fields (McCleave and Power 1978), magnetic fields (Walker 1984), gyres (Williams 1972), and pheromones (Nordeng 1977). Certain characteristics of these isolated, open-ocean seamounts may promote their detection by armorhead. First, current-topography interactions may create significant signals in physical and biological features. The region of the SE-NHR seamounts is active in front development (Roden and Paskausky 1978); upwelling, eddies, and other aspects of flow complexity also occur around these seamounts (Roden et al. 1982) and downstream from them (Royer 1978). The biological signals may include increased chlorophyll in response to upwelling or doming of isotherms (Genin and Boehlert 1985), or aggregations of various organisms and the larger animals which prey upon them around seamounts (see review in Boehlert and Genin 1987). Gravity anomalies associated with seamounts may also play a role; positive gravity anomalies exist at the summit and slopes, and negative anomalies are seen in the surrounding "moat" regions (Wedgeworth and Kellogg 1987). Seamounts often have strong magnetic dipoles associated with them, and the dipole might serve as a landmark for magnetic orientation by fish (Klimley[7]). While fish have been shown to have magnetoreceptors (Walker et al. 1985), their use of magnetic maps remains speculative but possible (Gould 1985). Although we cannot postulate the mechanism that armorhead use for recruitment, it is clear that the effects of seamounts may be detected at distances greater than their area alone would suggest.

## Interannual Variations in Recruitment Strength

The year-class strength of armorhead recruiting to seamounts appears to be independent of the parent stock size (Wetherall and Yong 1986). As an example, Borets (1975) estimated that on the SE-NHR seamounts from 1968 to 1973, the stock size varied by a factor of <1.8 while recruitment varied by >5.5 times. The relative abundance of armorhead at the SE-NHR seamounts area increased in 1986 after a long period at a very low level. This increase probably corresponds to the high abundance of pelagic specimens captured in the northeastern Pacific in 1985 (Fig. 2B; Table 2) that consisted of two age groups. The increased recruitment at the SE-NHR seamounts in 1986 suggests that environmental conditions were favorable to the survival of young armorhead in the 1984 and 1985 winter seasons.

A wide variety of factors, both biotic and physical, can affect survival and ultimate year-class strength in fishes (Lasker 1978). During the 2 years between spawning and recruitment for armorhead, an extended migration through varied pelagic environments occurs (Fig. 4). Feeding conditions for larval and juvenile stages are characterized by interannual variability; Fedosova (1980) suggested that warm years were more productive for zooplankton prey and, thus, favorable to the survival of young armorhead. Interannual variation in atmospheric systems (Seckel 1988) or large-scale ocean currents of the kind described by Mysak et al. (1982) may also play a role in armorhead recruitment strength. Changes in the position of the Alaska gyre by up to 700 km southwest of its normal position may have occurred from 1981 to 1985, with an associated increase in seawater temperature (Royer and Emery 1987). Large-scale atmospheric phenomena, such as the longitudinal position of the Aleutian Low, may create definite interannual variations in winter wind systems that may be seen in surface current patterns (Seckel 1988). These patterns may, in turn, be related to the latitudinal position of the subtropical front, which varies interannually between lat. 28° and 32°N (Roden 1970). Variability in these features influences surface drift (McNally 1981), which in turn affects the neustonic young of armorhead. If flow in certain years results in transport of armorhead to other regions (such as the western Pacific or the southern part of the northeast Pacific; Fig. 4), it is possible that large-scale mortalities of armorhead occur later in life, resulting in weak year classes at the SE-NHR seamounts.

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[7] P. Klimley, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. 30 June 1987.

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## LITERATURE CITED

ABE, T.
1957. New, rare or uncommon fishes from Japanese [waters]. VI. Notes on the rare fishes of the family Histiopteridae. Jpn. J. Ichthyol. 6:35–39, 71–74.
1969. Notes on some edible marine fishes collected between the Bonin Islands and the mouth of Sagami Bay—III. Bull. Tokai Reg. Fish. Res. Lab. 60:5–8.

ALTON, M. S.
1986. Fish and crab populations of Gulf of Alaska seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 45–51. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

BILIM, L. A., L. A. BORETS, AND L. K. PLATOSHINA.
1978. Characteristics of ovogenesis and spawning of the boarfish in the region of the Hawaiian Islands. *In* Fisheries oceanography, hydrobiology, biology of fishes and other denizens of the Pacific Ocean, p. 51–57. Izv. Pac. Ocean Sci. Res. Inst. Fish. Oceanogr. (TINRO), Vladivostok, 102. (Engl. transl. by W. G. Van Campen, 1986, 9 p., Transl. No. 106; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

BOEHLERT, G. W.
1986. Productivity and population maintenance of seamount resources and future research directions. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 95–101. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

BOEHLERT, G. W., AND A. GENIN.
1987. A review of the effects of seamounts on biological processes. *In* B. Keating, P. Fryer, R. Batiza, and G. W. Boehlert (editors), Seamounts, islands, and atolls, p. 319–334. Geophys. Monogr. 43.

BORETS, L. A.
1975. Some results of studies on the biology of the boarfish (*Pentaceros richardsoni* Smith). Invest. Biol. Fishes Fish. Oceanogr., TINRO, Vladivostok 6:82-90. (Engl. transl. by W. G. Van Campen, 1984, 9 p., Transl. No. 97; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)
1976. The state of the boarfish, *Pentaceros richardsoni* (Smith) stock in the Hawaii submersive range areas. Invest. Biol. Fishes Fish. Oceanogr., TINRO, Vladivostok 7:58–62. (Engl. transl. by W. G. Van Campen, 1987, 5 p., Transl. No. 112; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)
1979. The population structure of the boarfish, *Pentaceros richardsoni*, from the Emperor Seamounts and the Hawaiian Ridge. J. Ichthyol. 19:15–20.

BORETS, L. A., AND A. S. SOKOLOVSKY.
1978. Species composition of the ichthyoplankton of the Hawaiian submarine ridge and the Emperor Seamounts. *In* Fisheries oceanography, hydrobiology, biology of fishes and other denizens of the Pacific Ocean, p. 43–50. Izv. Pac. Ocean Sci. Res. Inst. Fish. Oceanogr. (TINRO), Vladivostok, Vol. 102. (Engl. transl. by W. G. Van Campen, 1986, 10 p., Transl. No. 105; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

CHELTON, D. B.
1984. Commentary: Short-term climatic variability in the northeast Pacific Ocean. *In* W. G. Pearcy (editor), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 87–99. Oreg. State Univ. Sea Grant, ORESU-W-83-001.

CHIKUNI, S.
1970. On gregarious fish, *Pseudopentaceros richardsoni* (Histiophoridae). Enyo (Far Seas) Fish. Res. Lab. News 3:1–4. (Engl. transl., The "phantom fish," "kusakari tsubodai"—an outline, by J. H. Shohara, 7 p.; available Natl. Mar. Fish. Serv., NOAA, Terminal Island, CA 90731.)

CLEMENS, W. A., AND G. V. WILBY.
1961. Fishes of the Pacific coast of Canada. 2d ed. Bull. Fish. Res. Board Can. 68, 443 p.

DARNITSKY, V. B., B. L. BOLDYREV, AND A. F. VOLKOV.
1984. Environmental conditions and some ecological characteristics of fishes from the central North Pacific seamounts. *In* P. A. Moiseev (editor), Proceedings, conditions of formation of commercial fish concentrations, p. 64–77. Minist. Fish., U.S.S.R., All-Union Res. Inst. Mar. Fish. Oceanogr. VNIRO. (Engl. transl. by W. G. Van Campen, 1987, 12 p., Transl. No. 114; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

EMERY, W. J., T. C. ROYER, AND R. W. REYNOLDS.
1985. The anomalous tracks of North Pacific drifting buoys 1981 to 1983. Deep-Sea Res. 32:315–347.

FAVORITE, F.
1967. The Alaskan Stream. Int. N. Pac. Fish. Comm. Bull. 21, 20 p.

FAVORITE, F., A. J. DODIMEAD, AND K. NASU.
1976. Oceanography of the subarctic Pacific region, 1960–1971. Int. N. Pac. Fish. Comm. Bull. 33, 187 p.

FEDOSOVA, R. A.
1980. Inter-year changes in the mesoplankton of the waters of the submarine banks of the Hawaiian Ridge (Northwestern Pacific Ocean). [In Russ.] Izv. Pac. Ocean Sci. Res. Inst. Fish. Oceanogr. (TINRO), Vladivostok 104:84–87.

FEDOSOVA, R. A., AND O. E. KOMRAKOV.
1975. Feeding of *Pentaceros richardsoni* frys in the Hawaiian region. [In Russ.] Invest. Biol. Fishes Fish. Oceanogr., TINRO, Vladivostok 6:52–55. (Engl. transl. by W. G. Van Campen, 1985, 4 p., Transl. No. 100; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

FOLLETT, W. I., AND L. J. DEMPSTER.
1963. Relationships of the percoid fish *Pentaceros richardsoni* Smith, with description of a specimen from the coast

of California. Proc. Calif. Acad. Sci., 4th Ser. 32(10):315–338.

FUJII, E.
1986. Zoogeographical features of fishes in the vicinity of seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 67–70. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

GENIN, A., AND G. W. BOEHLERT.
1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. J. Mar. Res. 43:907–924.

GOULD, J. L.
1985. Are animal maps magnetic? *In* J. L. Kirschvink, D. S. Jones, and B. J. MacFadden (editors), Magnetite biomineralization and magnetoreception in organisms, p. 257–268. Plenum Press, N.Y.

HARDY, G. S.
1983. A revision of the fishes of the family Pentacerotidae (Perciformes). N.Z. J. Zool. 10:177–220.

HONMA, Y., AND R. MIZUSAWA.
1969. A record of the young of boar fish, *Pseudopentaceros richardsoni*, from North Pacific. Jpn. J. Ichthyol. 15:134–136.

HUGHES, S. E.
1981. Initial U.S. exploration of nine Gulf of Alaska seamounts and their associated fish and shellfish resources. Mar. Fish. Rev. 43(1):26–33.

HUMPHREYS, R. L., JR., AND D. T. TAGAMI.
1986. Review and current status of research on the biology and ecology of the genus *Pseudopentaceros*. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 55–62. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

HUMPHREYS, R. L., JR., G. WINANS, AND D. T. TAGAMI.
In press. Synonomy and proposed life history of the North Pacific pelagic armorhead, *Pseudopentaceros wheeleri* Hardy (Pisces: Pentacerotidae). Copeia 1988.

IGNELL, S., J. BAILEY, AND J. JOYCE.
1986. Observations on high-seas squid gill-net fisheries, North Pacific Ocean, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-105, 52 p.

JAPAN MARINE FISHERY RESOURCE RESEARCH CENTER.
1980. Report of exploratory fishing of Pacific pomfret. Jpn. Mar. Fish. Resour. Res. Cent. Rep. 53-16.
1983a. Report of exploratory fishing of Pacific pomfret. Jpn. Mar. Fish. Resour. Res. Cent. Rep. 54-18.
1983b. Report of exploratory fishing of Pacific pomfret. Jpn. Mar. Fish. Resour. Res. Cent. Rep. 55-16.
1985. Report of exploratory fishing of Pacific pomfret. Jpn. Mar. Fish. Resour. Res. Cent. Rep. 57-12.

KAWAMURA, A.
1982. Food habits and prey distributions of three rorqual species in the North Pacific Ocean. Sci. Rep. Whales Res. Inst. 34:59–91.

KIRWAN, A. D., JR., G. H. MCNALLY, E. REYNA, AND W. J. MERRELL, JR.
1978. The near-surface circulation of the eastern North Pacific. J. Phys. Oceanogr. 8:937–945.

KOMRAKOV, O. E.
1970. Distribution and fishery of the boarfish (*Pentaceros richardsoni* Smith) in the Hawaiian region. In the collection: The present state of biological productivity and the volume of biological resources of the world ocean and prospects for their utilization. Kaliningrad, p. 155–163. (Engl. transl. by W. G. Van Campen, 1987, 9 p., Transl. No. 117; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

LARKINS, H. A.
1964. Some epipelagic fishes of the North Pacific Ocean, Bering Sea, and Gulf of Alaska. Trans. Am. Fish. Soc. 93:286–290.

LASKER, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–230.

LUTJEHARMS, J. R. E., AND A. E. F. HEYDORN.
1981. Recruitment of rock lobster on Vema Seamount from the islands of Tristan da Cunha. Deep-Sea Res. 28A:1237.

MACY, P. Y., J. M. WALL, N. D. LAMPSAKIS, AND J. E. MASON.
1978. Resources of non-salmonid pelagic fishes of the Gulf of Alaska and eastern Bering Sea. Parts 1–3, Final Rep. BLM/OCSEAP Contracts R7120811 and R7120812, Northwest and Alaska Fish. Cent., NMFS, NOAA, Seattle, Wash.

MCCLEAVE, J. D., AND J. H. POWER.
1978. Influence of weak electric and magnetic fields on turning behavior in elvers of American eel *Anguilla rostrata*. Mar. Biol. (Berl.) 46:29–34.

MCNALLY, G. J.
1981. Satellite-tracked drift buoy observations of the near-surface flow in the eastern mid-latitude North Pacific. J. Geophys. Res. 86:8022–8030.

MCNALLY, G. J., W. C. PATZERT, A. D. KIRWAN, JR., AND A. C. VASTANO.
1983. The near-surface circulation of the North Pacific using satellite tracked drifting buoys. J. Geophys. Res. 88:7505–7518.

MYSAK, L. A., W. W. HSIEH, AND T. R. PARSONS.
1982. On the relationship between interannual baroclinic waves and fish populations in the northeast Pacific. Biol. Oceanogr. 2:63–103.

NORDENG, H.
1977. A pheromone hypothesis for homeward migration in anadromous salmonids. Oikos 28:155–159.

OKAMURA, I., K. AMAOKA, AND F. MITANI (editors).
1982. Fishes of the Kyushu-Palau Ridge and Tosa Bay. Jpn. Fish. Res. Conserv. Assoc., Tokyo, 435 p.

RANDALL, J. E.
1980. New records of fishes from the Hawaiian Islands. Pac. Sci. 34:211–232.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.

ROBINSON, S. M. C., AND G. S. JAMIESON.
1984. Report on a Canadian commercial fishery for flying squid using drifting gill nets off the coast of British Columbia. Can. Ind. Rep. Fish. Aquat. Sci. 150, 25 p.

RODEN, G. I.
1970. Aspects of the mid-Pacific transition zone. J. Geophys. Res. 75:1097–1109.

RODEN, G. I., AND D. F. PASKAUSKY.
1978. Estimation of rates of frontogenesis and frontolysis in the North Pacific Ocean using satellite and surface meteorological data from January 1977. J. Geophys. Res. 83:4545–4550.

RODEN, G. I., B. A. TAFT, AND C. C. EBBESMEYER.
1982. Oceanographic aspects of the Emperor Seamounts region. J. Geophys. Res. 87:9537–9552.

ROYER, T. C.
1978. Ocean eddies generated by seamounts in the North Pacific. Science (Wash., D.C.) 199:1063–1064.

ROYER, T. C., AND W. J. EMERY.
1987. Circulation in the Gulf of Alaska, 1981. Deep-Sea Res. 34:1361–1377.
SASAKI, T.
1974. Kita Taiheiyo no kusakari tsubodai (The pelagic armorhead, *Pentaceros richardsoni* Smith, in the North Pacific). Bull. Jpn. Soc. Fish. Oceanogr. 24:156–165. (Engl. transl. by T. Otsu, 1977, 13 p., Transl. No. 16; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)
1986. Development and present status of Japanese trawl fisheries in the vicinity of seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 21–30. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.
SECKEL, G. R.
1988. Indices for mid-latitude North Pacific winter wind systems; an exploratory investigation. GeoJournal 16:97–111.
SHIMAZAKI, K., AND S. NAKAMURA.
1981. Ecological studies of the pomfret (*Brama japonica* Hilgendorf). I. The seasonal distribution pattern and ecological considerations. Res. Inst. N. Pac. Fish., Spec. Vol., p. 91–103.
SLOAN, N. A.
1983. Canadian-Japanese experimental fishery for oceanic squid off British Columbia, summer 1983. Can. Ind. Rep. Fish. Aquat. Sci. 152, 42 p.
SMITH, J. G.
1965. A second record of the pelagic armorhead, *Pentaceros richardsoni* Smith, 1849, in California waters. Calif. Fish Game 51:213–214.
TAKAHASHI, Y., AND T. SASAKI.
1977. Kita Taiheiyo chubu kaizan ni okeru tororu gyogyo (Trawl fishery in the central North Pacific seamounts). Northern Waters Groundfish Resour., Far Seas Fish. Res. Lab., 45 p. (Engl. Transl. by T. Otsu, 1977, 49 p.; Transl. No. 22; available Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)
UCHIDA, R. N., AND D. T. TAGAMI.
1984. Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev. 46(2): 1–17.
UDA, M., AND K. HASUNUMA.
1969. The eastward subtropical countercurrent in the western North Pacific Ocean. J. Oceanogr. Soc. Jpn. 25:201–210.
WAGNER, E. J., AND C. E. BOND.
1961. The percoid fish *Pseudopentaceros richardsoni* from Oregon waters. Fish. Comm. Oreg., Res. Briefs 8(1):71–73.
WALKER, M. M.
1984. Magnetic sensitivity and its possible physical basis in the yellowfin tuna, *Thunnus albacares*. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (editors), Mechanisms of migration in fishes, p. 125–142. Plenum Press, N.Y.
WALKER, M. M., J. L. KIRSCHVINK, AND A. E. DIZON.
1985. Magnetoreception and biomineralization of magnetite. Fish. *In* J. L. Kirschvink, D. S. Jones, and B. J. MacFadden (editors), Magnetite biomineralization and magnetoreception in organisms, p. 417–437. Plenum Press, N.Y.
WEDGEWORTH, B., AND J. KELLOGG.
1987. A 3-D gravity-tectonic study of Ita Mai Tai Guyot: an uncompensated seamount in the East Mariana Basin. *In* B. Keating, P. Fryer, R. Batiza, and G. W. Boehlert (editors), Seamounts, islands, and atolls, p. 73–84. Geophys. Monogr. 43.
WELANDER, A. D., R. C. JOHNSON, AND R. A. HAJNY.
1957. Occurrence of the boarfish, *Pseudopentaceros richardsoni*, and the zeid, *Allocyttus verrucosus*, in the North Pacific. Copeia 1957:244–246.
WETHERALL, J. A., AND M. Y. Y. YONG.
1986. Problems in assessing the pelagic armorhead stock on the central North Pacific Seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 73–85. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.
WILLIAMS, F.
1972. Consideration of three proposed models of the migration of young skipjack tuna (*Katsuwonus pelamis*) into the eastern Pacific Ocean. Fish. Bull., U.S. 70:741–762.
ZAMA, A., M. ASAI, AND F. YASUDA.
1977. Records of the pelagic armorhead, *Pentaceros richardsoni* from Hachijo Island and the Ogasawara Islands. Jpn. J. Ichthyol. 24:57–60.

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# DYNAMIC RESPONSE ANALYSIS. III. A CONSISTENCY FILTER AND APPLICATION TO FOUR NORTHERN ELEPHANT SEAL COLONIES

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## ABSTRACT

Dynamic response analysis, a technique for determining stock size relative to the maximum net productivity level (MNPL), was applied to northern elephant seal populations from the South Farallon Islands, Año Nuevo Island, San Nicolas Island and San Miguel Island. Pup counts were used as indices of population size. The application of dynamic response analysis presented here involved some methodological innovations. We present a moving interval method which involves calculating separate dynamic response analyses for intervals of various lengths ranging from four counts to the total number available for the colony. The sign of the second order polynomial regression coefficient computed from a particular interval was used to indicate the colony's apparent status (relative to its MNPL; + = above MNPL, − = below MNPL) on that interval. Consistency in the sign of the second order coefficient, as the interval was moved along the trajectory, was used to determine the minimum reliable interval size. Each colony exhibited growth similar to that of a population below its MNPL. These results are consistent with recent natural history observations at San Nicolas, San Miguel and the South Farallon islands. Natural history observations at Año Nuevo Island suggest that the colony there is now at equilibrium. Thus, if our results from dynamic response analysis of the Año Nuevo colony are correct, it appears that the MNPL may be close to the carrying capacity for these animals.

Key words: dynamic response analysis, *Mirounga angustirostris*, maximum net productivity level, population dynamics, stock assessment.

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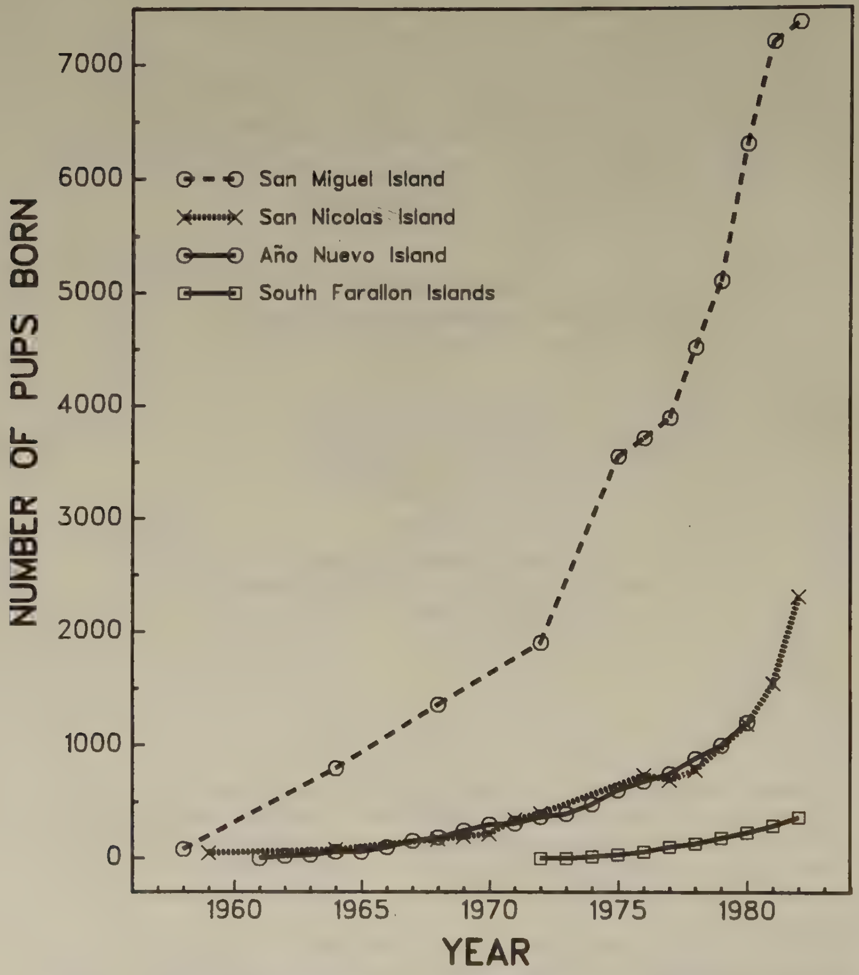

*Figure 1.* Numbers of northern elephant seal pups born on San Miguel, San Nicolas, Año Nuevo and Southeast Farallon islands. Literature sources of the censuses are cited in the text.

Dynamic response analysis is a technique for assessment of the size of a stock relative to its maximum net productivity level (MNPL). The theory and derivation of the dynamic response method are presented by Goodman (1988). Gerrodette (1988) evaluated the performance of the method when applied to simulated unharvested populations. This study is an application of dynamic response analysis to census data from colonies of northern elephant seals (*Mirounga angustirostris*).

The form of a dynamic response analysis depends on whether the population is harvested and on how far the population is from equilibrium (Goodman 1988). Here we use the dynamic response method to analyze four elephant seal colonies (Fig. 1), which have been unharvested, and growing rapidly, since recolonization several decades ago (*e.g.*, Le Boeuf 1977, Antonelis *et al.* 1981, Cooper and Stewart 1983). As it is unlikely that carrying capacity for these populations is expanding in this fashion, the rapid, steady growth suggests that the colonies have not yet reached their equilibrium densities.

Unharvested populations such as these, in a constant environment, will have growth rates which increase over time when the densities are below MNPL, producing trajectories of population size that are concave upward. Growth in the range of densities above MNPL will produce trajectories which are concave downward. These characteristic shapes imply that for an unharvested population growing from low initial density, a dynamic response analysis is equivalent to determining whether the trajectory of population levels is concave upward, concave downward, or not significantly curved. This determination can be accomplished by fitting the trajectory to a nonlinear model (*e.g.*, by polynomial regression) and testing the appropriate fitted parameters.

To make the determination as relevant as possible to the present state of the population (for management purposes), only recent censuses should be used. On the other hand, it is important to base the determination on curvature in the trajectory which is due to density dependent changes in the population growth rate, rather than apparent curvature due to environmental variation or census inaccuracy, so the number of censuses must not be too small. The values for parameters which Gerrodette (1988) used to determine census requirements (model for growth, level of census precision and amount of environmental variation) are unknown for the elephant seal population. Therefore, we present a method which uses the variation in the entire trajectory to estimate the minimum number of the recent censuses which need to be included for a reliable assessment. The recent status of the population relative to its MNPL is then determined from the curvature in the interval spanned by this minimum number of most recent censuses.

## METHODS

*Statistical approach*—We computed multiple linear regressions of pups born versus time and that time squared. The regressions were calculated for intervals ranging from four censuses to the total number of censuses available for that colony. For each interval size, the intervals were moved along the trajectory in steps, at each step adding a more recent census, discarding the oldest census, and computing the regression. Thus, for $n$ total points available, and an interval size of $k$ points, there would be $n - k + 1$ separate regressions.

Each regression is a least squares fit to a second degree polynomial. This model was chosen because the direction of concavity is determined simply by the sign of the second order coefficient. A significantly positive second order term means the census interval is concave upward; a significantly negative second order term means the concavity is downward; and a second order term not significantly different from zero means the interval cannot be distinguished from a linear trajectory. A coefficient was taken to be significantly positive if it was more than two standard errors (Sokal and Rohlf 1981, p. 636) greater than

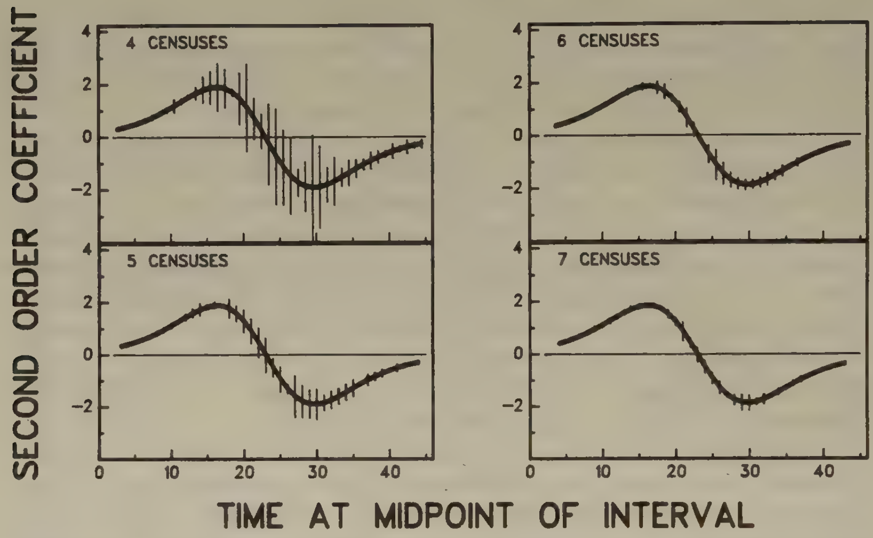

*Figure 2.* Second order regression coefficients computed from a hypothetical logistic population trajectory using intervals of from 4 to 7 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus two or minus standard errors of the coefficients.

zero, and negative if more than two standard errors less than zero. All other values were considered not significantly different from zero.

The $(n - k + 1)$ second order coefficients for a given value of $k$ (number of censuses per interval) were plotted against the times of the midpoints of the respective census intervals. We interpreted the results on the basis of the expected qualitative form of a plot of second order regression coefficients from a density dependent growth curve with no environmental variation and no census error. Figure 2 shows plots of the second order regression coefficients obtained by applying our moving interval method to a hypothetical, deterministic population trajectory generated from the well known logistic model. When population size is small, the regression coefficients are positive, reflecting the upward concavity in the growth curve; as population size increases, the regression coefficients decrease and become indistinguishable from zero when the population reaches MNPL; finally, the coefficients take on negative values at population sizes above MNPL.

The details of the shapes of the curves in Figure 2 are dependent on the logistic model used to generate the hypothetical trajectory. For dynamic response analysis, the important (and more general) feature of this expected form is that the curve formed by the coefficients crosses zero only once as the population grows from low density to equilibrium. This feature is not model dependent. Deviations from this form in the plots of regression coefficients computed from real trajectories will indicate that the regressions are revealing local curvature which is due to processes other than density dependent growth from a condition below carrying capacity in a constant environment.

In practice, we need to find the smallest interval size which yields a plot of second order coefficients that does not exhibit the features of responding mainly to environmental noise or census error. In other words, the curve formed by the second order coefficients should cross the zero line a maximum of one time and in a prescribed direction. The minimum interval size which still allows for statistical tests in a second degree polynomial model (three parameters) is four censuses. If the second order coefficients based on intervals of four censuses cross the zero line more than once, the interval size is increased to five counts, and so on until the curve formed by the coefficients crosses the zero line either once, or not at all.

The vertical bars in Figure 2 represent plus or minus two estimated standard errors of the regression coefficients. Because there was no environmental variation or census error in the underlying logistic model, these error bars represent uncertainty in the regression coefficients introduced by using a quadratic polynomial to fit portions of a logistic curve. The uncertainty is substantial with four censuses per interval but diminishes rapidly when five or more censuses are used. By using the quadratic model in ''local'' analyses of the shapes of portions of the trajectory, we avoid the need to assume a specific model for the entire trajectory which would put constraints on the location of the MNPL (Goodman 1988).

In a sensitivity analysis of the dynamic response method, Gerrodette (1988) showed that a two-step procedure (testing the significance of a linear regression on the census interval and then testing for curvature with a polynomial regression only if the linear slope was significantly positive) gave higher proportions of correct determinations over a broad range of population sizes than simply considering the direction of curvature. This two-step procedure was not used in the stage of our method where we determined the correct number of censuses to use based on plots of second order terms. However, for making the decision about status relative to the MNPL, we tested for a significantly positive slope of a linear regression on those censuses prior to evaluating the direction and significance of the curvature.

*Data set*—Because dynamic response analysis depends on the shape of the population trajectory, rather than the actual population size, an index which is approximately a scalar multiple of total population size will suffice (Goodman 1988). We used published counts of northern elephant seal pups born at four rookeries (Fig. 1) as indices of population sizes. The 11 pup counts from the South Farallon Islands are from Huber *et al.* (1983). There are 20 published counts from Año Nuevo Island (Orr and Poulter 1965, Radford *et al.* 1965, Rice *et al.* 1965, Le Boeuf and Briggs 1977, Le Boeuf and Bonnell 1980, Reiter *et al.* 1981). The 13 counts from San Nicolas Island are from Bartholomew and Boolootian (1960), Odell (1971, 1974), Antonelis *et al.* (1981), Le Boeuf (1977), Le Boeuf and Bonnell (1980) and Stewart and Yochem (1984). The 12 counts from San Miguel Island are from Bartholomew and Boolootian (1960), Odell (1974), Le Boeuf (1977), Antonelis *et al.* (1981), Mate (1977), Le Boeuf and Bonnell (1980), Bonnell *et al.* (1980) and Cooper and Stewart (1983). Cooper and Stewart (1983) estimated the per capita growth rates to be 0.136 at San Miguel Island, 0.165 at San Nicolas Island, 0.158 at Año Nuevo Island, and 0.533 at the Farallons (the latter rate was attributed mostly to immigration).

We assume that the proportion of pups in the total population is constant. This constancy of age structure is not likely in a population growing under density dependence. In simulations of growth of closed populations, Birkson and DeMaster (1985) evaluated the practical reliability of pup counts as population indices and found slight biases, the directions of which depend on whether the pup census precedes or follows a period of density dependent survival. Elephant seal pup mortality between birth and weaning appears to be density dependent (Reiter *et al.* 1981, Huber *et al.* 1983). According to Birkson and DeMaster (1985), this implies that the population should reach its MNPL before the pup trajectory would indicate that the MNPL had been reached. However, the probability of a pregnant female hauling out to pup on a particular island may be density dependent as well (Reiter *et al.* 1981). Thus, there may be density dependent processes both preceding and following the censuses used in this study and the resulting direction of bias cannot be predicted.

In light of the considerable importance of immigration by breeding age animals contributing to growth of some elephant seal colonies (*e.g.*, Huber *et al.* 1983), there is a further disturbance of age structure. For lack of reliable adult censuses, the degree of deviation from the stable age distribution is unknown. For purposes of exploring the methodology, we have proceeded with this data set as if the proportionality assumption were met, but for the purpose of conducting an actual assessment of the elephant seal populations, the problem of age structure would require further examination.

We have used the terms 'colony' and 'population' interchangeably. We recognize that the breeding colonies are probably not distinct populations, but we assume that the density dependent responses to growth by reproduction and by immigration combine in such a way that the production curve ($dN/dt$ *vs.* $N$) is smoothly unimodal over the region of interest and that it correctly reflects the implicit concerns of status assessment under the Marine Mammal Protection Act (MMPA).

The method we present can absorb year-to-year variation or "noise" in the environment but not long-term systematic environmental change. Therefore, we assume that the MNPL has maintained a stationary mean (though not that the MNPL was necessarily constant) during the time spanned by the censuses.

## RESULTS

Figures 3–6 show series of plots of the second order regression coefficients computed from various sizes of census intervals for each colony. These plots were compared to the expected qualitative form (*e.g.*, that of plots in Fig. 2) to determine the appropriate number of censuses to use for the dynamic response analyses.

*Año Nuevo Island*—When an interval of four censuses is moved along the Año Nuevo trajectory, the second order regression coefficient computed at each

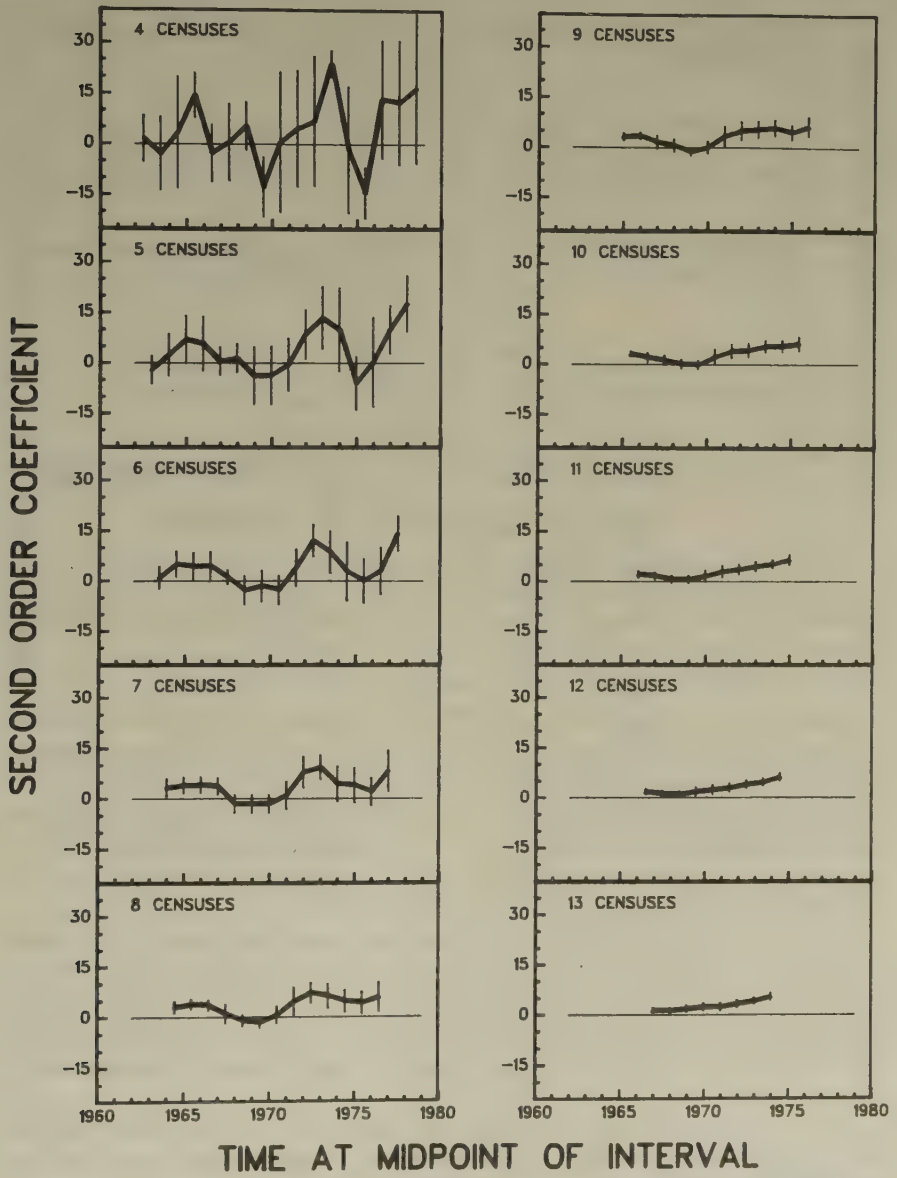

*Figure 3.* Second order regression coefficients computed from the Año Nuevo Island pup count trajectory using intervals of from 4 to 13 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus or minus two standard errors of the coefficients.

step fluctuates over a broad range of positive and negative values (Fig. 3). This variation in the curvature suggests that intervals of four censuses are insufficient for distinguishing between curvature due to density dependence and that due to environmental variation or census error.

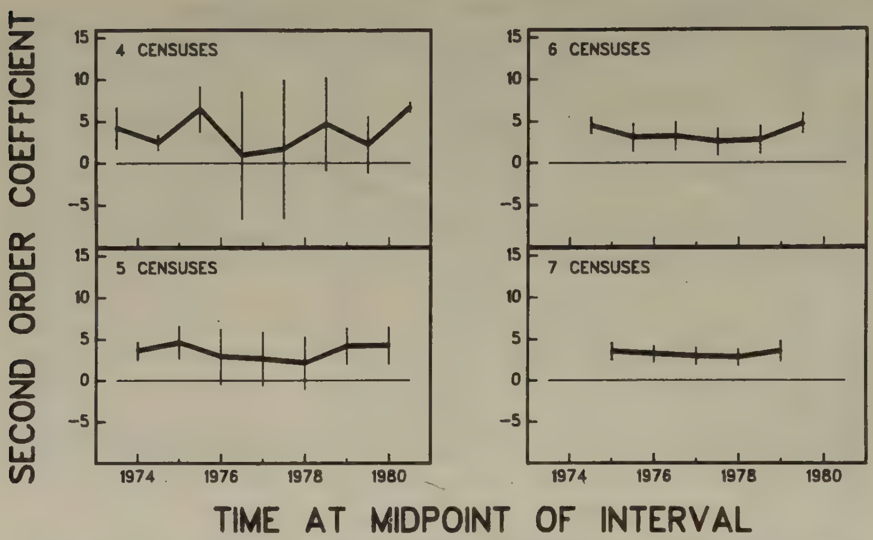

*Figure 4.* Second order regression coefficients computed from the Farallon Islands pup count trajectory using intervals of from 4 to 7 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus or minus two standard errors of the coefficients.

Using intervals ranging in size from 5 to 11 censuses, at Año Nuevo, reduces the variation in the curvature; but in every case, the second order coefficients drop from positive to zero and then become positive on the most recent intervals (Fig. 3). Only when 12 or more points are included are the coefficients consistent with our requirement that the plot of the coefficients cross zero either once or not at all, leading us to conclude that 12 is the minimum number of censuses required for a reliable assessment of the Año Nuevo Island colony.

*South Farallon Islands*—When four or five censuses are used in regressions on the South Farallon Island pup counts, the coefficients fluctuate between positive values and values which are not distinguishable from zero (Fig. 4). Using intervals of six censuses results in second order coefficients which are all positive and we conclude that we must use at least six censuses for an assessment of this colony.

*San Nicolas Island and San Miguel Island*—For San Nicolas Island (Fig. 5), the minimum number of censuses providing an unambiguous result is nine. For San Miguel Island (Fig. 6), the minimum number is eight.

Having chosen the appropriate sequence of pup counts for each colony, the actual dynamic response analysis consists of testing the significance of the slope and curvature (Table 1) of the relationship between numbers of pups born and time. The slope coefficients from the linear regressions in Table 1 are significantly greater than zero for all four colonies, reflecting genuine increases in the sizes of the colonies with time. This is a condition which can occur when population sizes are above or below MNPL, so the direction and degree of curvature must be considered to make the determination (Gerrodette 1988). The second order

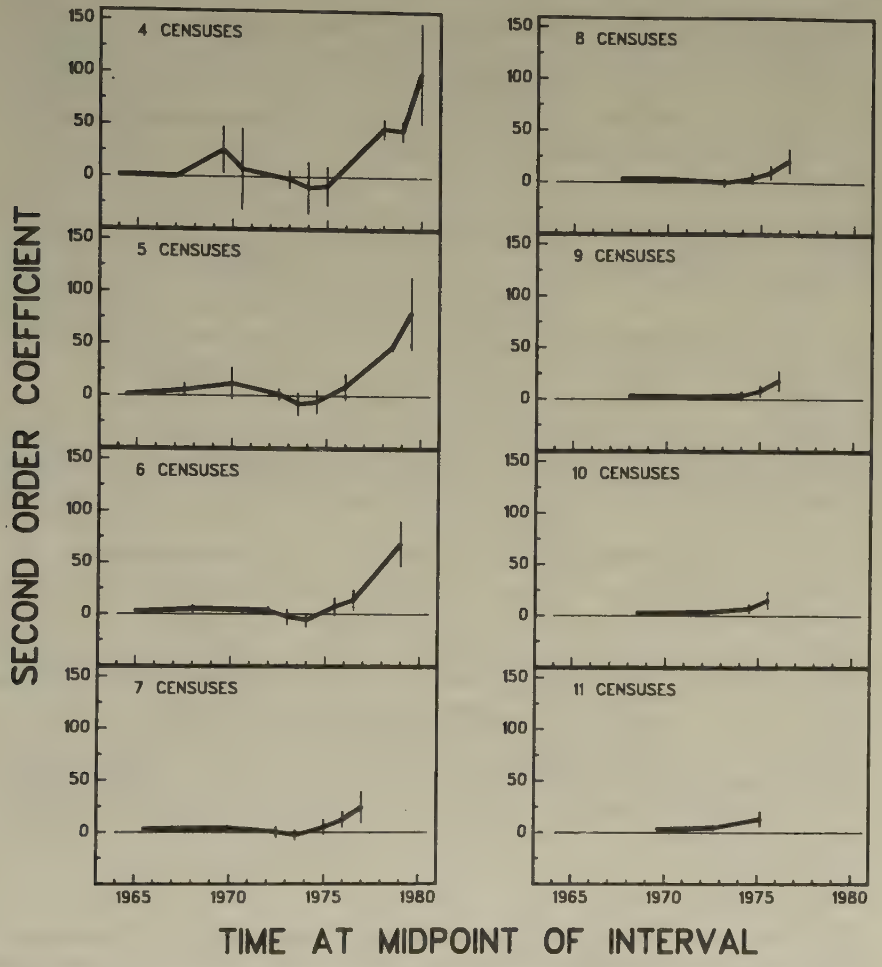

*Figure 5.* Second order regression coefficients computed from the San Nicolas Island pup count trajectory using intervals of from 4 to 11 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus or minus two standard errors of the coefficients.

coefficients in Table 1 are all greater than zero (at significance levels of 10% or less), reflecting upward curvature in the trajectories. We conclude that all four colonies exhibited growth, on the selected census intervals, like populations below their respective MNPLs.

## DISCUSSION

Gerrodette (1988) presented an example of how the decision process of dynamic response analysis could be formalized statistically for a particular set of assumptions about a model for growth, variability in the environment and census uncertainty. Although the method we present could also be cast in terms

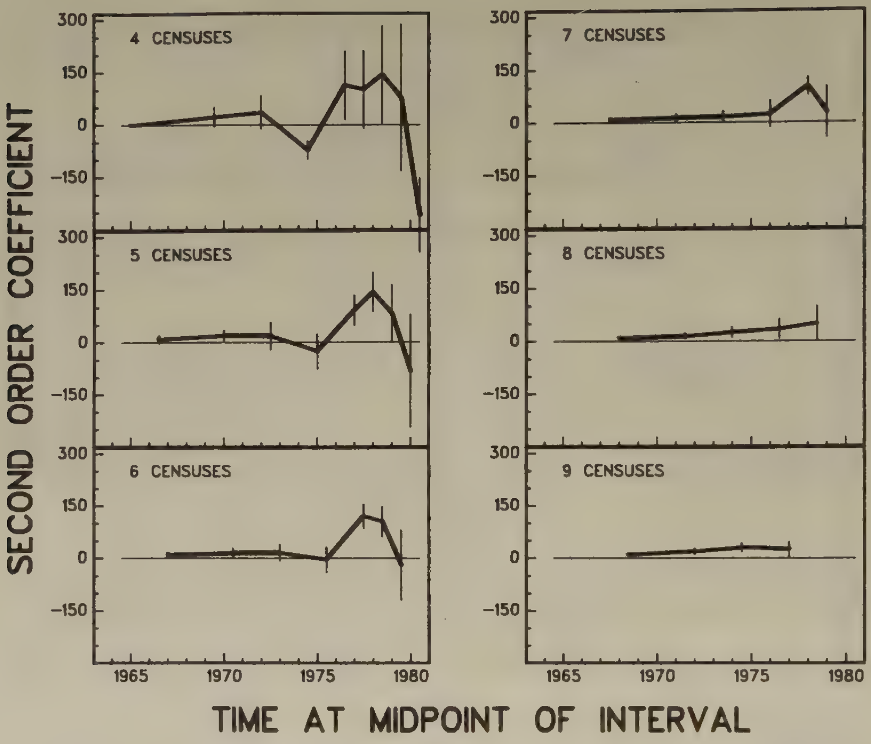

*Figure 6.* Second order regression coefficients computed from the San Miguel Island pup count trajectory using intervals of from 4 to 9 censuses. The coefficients were computed by moving the intervals along the trajectory in steps, computing a regression at each step. Error bars are plus two or minus standard errors of the coefficients.

*Table 1.* Results from separate linear and second degree polynomial regressions of pups born on time since breeding began, in years. The census interval was chosen by the moving interval method described in the text.

| Colony | Census interval | Number of censuses | Linear regression coefficient (std. error) | 2nd order regression coefficient (std. error) |
|---|---|---|---|---|
| Año Nuevo | 1969–1980 | 12 | +82.8***<br>(6.33) | +6.27***<br>(0.63) |
| S. Farallons | 1977–1982 | 6 | +52.6***<br>(3.55) | +4.75***<br>(0.59) |
| San Nicolas | 1970–1982 | 9 | +134***<br>(25.6) | +18.2**<br>(4.96) |
| San Miguel | 1975–1982 | 8 | +619***<br>(61.6) | +51.8*<br>(24.4) |

Two-tailed Student's $t$-tests of the hypothesis: coefficient = 0.
*** $P < .01$; ** $P < .05$; * $P < .10$.

of a statistically formal decision process, we attempted simply to minimize the probability of making an incorrect decision, subject to the constraint that the decision should be as current as the data allow.

Our final census intervals, ranging in size from six counts at the South Farallons to 12 counts at Año Nuevo, are similar to the requirements that Gerrodette (1988) found in his simulations (at least 10 censuses for probability of a correct decision to be generally greater than about 0.7). The relative smoothness of the curves in Figure 1 suggests that elephant seal pup counts may be less variable than census data for most species of marine mammals. If so, the data requirements for other species will probably be more stringent.

Recent data from San Nicolas and San Miguel islands (Stewart, unpublished data) and the Farallon Islands (H. Huber, personal communication) are consistent with our conclusion that these colonies are below their MNPLs. Condit and Le Boeuf (1983), however, suggested that the Año Nuevo colony had reached an equilibrium level in 1983 of approximately 1,000 breeding females and predicted that the colony would fluctuate around that level depending on environmental conditions.

The apparent inconsistency between these independent assessments of the status of the Año Nuevo colony draws attention to the trade-off associated with being certain versus being current. We note that increasing the number of censuses in the regression interval reduces the variation in the second order coefficients, but the midpoint of the most recent interval recedes into the past (*e.g.,* Fig. 3). In other words, the assessment becomes less current as more censuses are included. Thus, including 12 censuses in the regressions on Año Nuevo pup counts effectively centers the most recent assessment around 1975, even though we used censuses from Año Nuevo which were made as recently as 1980.

We consider it plausible that a colony such as Año Nuevo might progress from a level below MNPL to equilibrium in a span of about six to eight years. This would suggest that the MNPL was very close to the carrying capacity. In that case, the production curve ($dN/dt$ *vs.* $N$) would have a peak shifted far to the right (Eberhardt and Siniff 1977, Fowler 1981).

The primary mechanism of density dependent change in the rate of pups born at Año Nuevo is, apparently, limited space on the island for pregnant females to haul-out and give birth (Condit and Le Boeuf 1983). If this is the primary density dependent mechanism at San Nicolas and San Miguel islands, then these colonies may be far below their respective MNPLs and carrying capacities. However, if other density dependent mechanisms (*e.g.,* competition for limited food resources) are operating at these colonies, then MNPLs (and carrying capacities) may be reached before breeding space becomes limiting.

An actual application of dynamic response analysis of population status relative to the MNPL involves a trade-off between the desire to use many censuses for accuracy and the desire to make decisions which are current, and thus based on fewer counts. Our method for choosing an appropriate number of censuses resolves this trade-off by requiring consistency with assumptions about density dependent population growth.

Analysis of the selected census intervals showed that all four colonies were below their respective MNPLs. This conclusion is consistent with independent observations of the conditions of the colonies at the South Farallon Islands, San Nicolas Island and San Miguel Island. However, other studies have suggested that the Año Nuevo Island colony has already reached equilibrium density. The disparity between these results might be reconciled in terms of the time lag between the center of the interval (1975) upon which the dynamic response estimate is based and the apparent time of attainment of equilibrium (1983). This explanation implies a very rapid transition from MNPL to carrying capacity, which however, is consistent with some other speculations about density dependent growth in long-lived animals.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

ANTONELIS, G. A., S. LEATHERWOOD AND D. K. ODELL. 1981. Population growth and censuses of the northern elephant seal, *Mirounga angustirostris*, on the California Channel Islands, 1958–1978. Fishery Bulletin (U.S.) 79:562–567.

BIRKSON, J. M., AND D. P. DEMASTER. 1985. Use of pup counts in indexing population changes in pinnipeds. Canadian Journal of Fisheries and Aquatic Sciences 42:873–879.

BARTHOLOMEW, G. A., AND R. A. BOOLOOTIAN. 1960. Numbers and population structure of the pinnipeds on the California Channel Islands. Journal of Mammalogy 41: 366–375.

BONNELL, M. L., B. J. LE BOEUF, M. O. PIERSON, D. H. DETTMAN, D. G. FARRENS, C. B. HEATH, R. F. GANTT AND D. J. LARSEN. 1981. Pinnipeds of the Southern California Bight. *In* Marine mammals and seabird surveys of the Southern California Bight area 1975–1978. Vol. 3, Investigator's Report, Part 1. NTIS PB81-248-71. 535 pp.

CONDIT, R. S., AND B. J. LE BOEUF. 1983. Density dependent regulation of an elephant seal population. Page 19 *in* Abstracts of the Fifth Biennial Conference on the Biology of Marine Mammals, Boston, MA.

COOPER, C. F., AND B. S. STEWART. 1983. Demography of northern elephant seals, 1911–1982. Science 219:969–971.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.

FOWLER, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602–610.

GERRODETTE, T. 1988. Dynamic response analysis. II. Evaluation of dynamic response analysis in a simulated no-harvest case. Marine Mammal Science 4:196–209.

GOODMAN, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. Marine Mammal Science 4:183–195.

HUBER, H. R., R. MCELROY, R. BOEKELHEIDE AND P. HENDERSON. 1983. Studies of marine mammals at the Farallon Islands, 1981–1982. National Marine Fisheries Service, Administrative Report LJ-83-09C. Southwest Fisheries Center, La Jolla, CA.

LE BOEUF, B. J. 1977. Back from extinction? Pacific Discovery 30:1–9.

LE BOEUF, B. J., AND K. T. BRIGGS. 1977. The cost of living in a seal harem. Mammalia 41:167–195.

LE BOEUF, B. J., AND M. J. BONNELL. 1980. Pinnipeds of the California Channel Islands: abundance and distribution. Pages 475–493 *in* D. Power, ed. The California Islands: Proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

MATE, B. R. 1977. Aerial censusing of pinnipeds in the eastern Pacific for assessment of population numbers, migratory distributions, rookery stability, breeding effort, and recruitment. Final report to U.S. Marine Mammal Commission, Washington, D.C. NTIS PB-265 859.

ODELL, D. K. 1971. Censuses of pinnipeds breeding on the California Islands. Journal of Mammalogy 52:187–190.

ODELL, D. K. 1974. Seasonal occurrence of the northern elephant seal, *Mirounga angustirostris,* on San Nicolas Island, California. Journal of Mammalogy 55:81–95.

ORR, R. T., AND T. C. POULTER. 1965. The pinniped population of Año Nuevo Island, California. Proceedings of the California Academy of Sciences 32:377–404.

RADFORD, K. W., R. T. ORR AND C. L. HUBBS. 1965. Reestablishment of the northern elephant seal (*Mirounga angustirostris*) off central California. Proceedings of the California Academy of Science 31:601–612.

REITER, J., K. J. PANKEN AND B. J. LE BOEUF. 1981. Female competition and reproductive success in northern elephant seals. Animal Behavior 26:670–687.

RICE, D. W., K. W. KENYON AND D. LLUCH. 1965. Pinniped populations at Islas Guadalupe, San Benito and Cedros, Baja California, in 1965. Transactions of the San Diego Society of Natural History 14:73–84.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Co., San Francisco.

STEWART, B. S., AND P. K. YOCHEM. 1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980–1982. Bulletin of the Southern California Academy of Sciences 83:121–132.

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# Distribution and Diet of Cassin's Auklet and Common Murre in Relation to Central California Upwellings

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**Abstract**
Cassin's Auklets (*Ptychoramphus aleuticus*) and Common Murres (*Uria aalge*) nesting in California feed on euphausiids and fish whose life histories are adapted to coastal upwellings. Employing ship, aerial, and satellite observations, we determined responses in distribution and diet of these alcids to onset and variations in upwelling near the Farallon Islands. Birds and their prey aggregated at shorter spatial scales across the shelf than along it. Feeding centers persisted as long as 60 d, but auklet distribution changed within a few days in response to formation of an upwelling "filament." Diets changed slowly, differing before and after upwelling.

## Introduction

Concurrent studies of seabird abundance, prey availability, and the ocean environment have been relatively few, but this combination is necessary to understand seabird occurrence patterns. Usually one of the elements is missing, or the scales of measurement are mismatched. In some cases bird and prey concentrations were found to correlate locally and over larger areas (e.g., Bradstreet 1979; Brown 1980; Briggs *et al.* 1984; Schneider and Piatt, in press), but in others correlation at local scales was poor (Woodby 1984; Obst 1985).

Off the California coast, the frontal zone between the offshore California Current and continental-shelf upwellings constitutes the main habitat of some seabirds and limits the distribution (seaward or shoreward) of others. Colonies of Cassin's Auklet (*Ptychoramphus aleuticus*), a planktivore, occur at only three sites; upwellings and frontal formation recur frequently at these sites. Colonies of Common Murres (*Uria aalge*) exist at two of these sites, as well as at others where upwellings are frequent. The murre dives much deeper than the auklet (Tuck and Squires 1955; Krasnow and Sanger 1982; Dolphin and McSweeny 1983) and feeds on fish, squid, and zooplankton. Both alcids are abundant near their Farallon Islands breeding colonies (Fig. 1), where they feed primarily on euphausiids and rockfish during nesting season (Manuwal 1974; DGA, unpublished data). These prey are adapted to reproducing in the upwelling environment and probably move toward shore from seaward of the shelf with the onset of upwelling during spring (Parrish *et al.* 1981; PBA and SES, unpublished data).

## Methods

By concurrent use of ship and aerial surveys and satellite imagery during 1985, we attempted to determine responses of these two alcids to onset and variations in upwelling. Continuous daylight transects for seabirds were complemented by concurrent hydrographic data, and trawls provided a measure of rockfish and plankton abundance.

We sampled before and after establishment of persistent upwelling. Prior to 20 April, brief periods of upwelling and offshore transport were interrupted by south storms and coastal convergence. Following a strong "coast-wide wind pulse" from 21 to 25 April, upwelling recurred frequently in May and much of June. Heavy winds in mid-June intensified upwelling for 200 km north of Point Reyes, and a warm-core eddy, centered off the shelf, entrained some of this upwelled water into a long "filament" extending southwest. Where the cold water passed 40 km west of Point Reyes, strong thermal (and density) gradients marked the edges.

## Results and Discussion

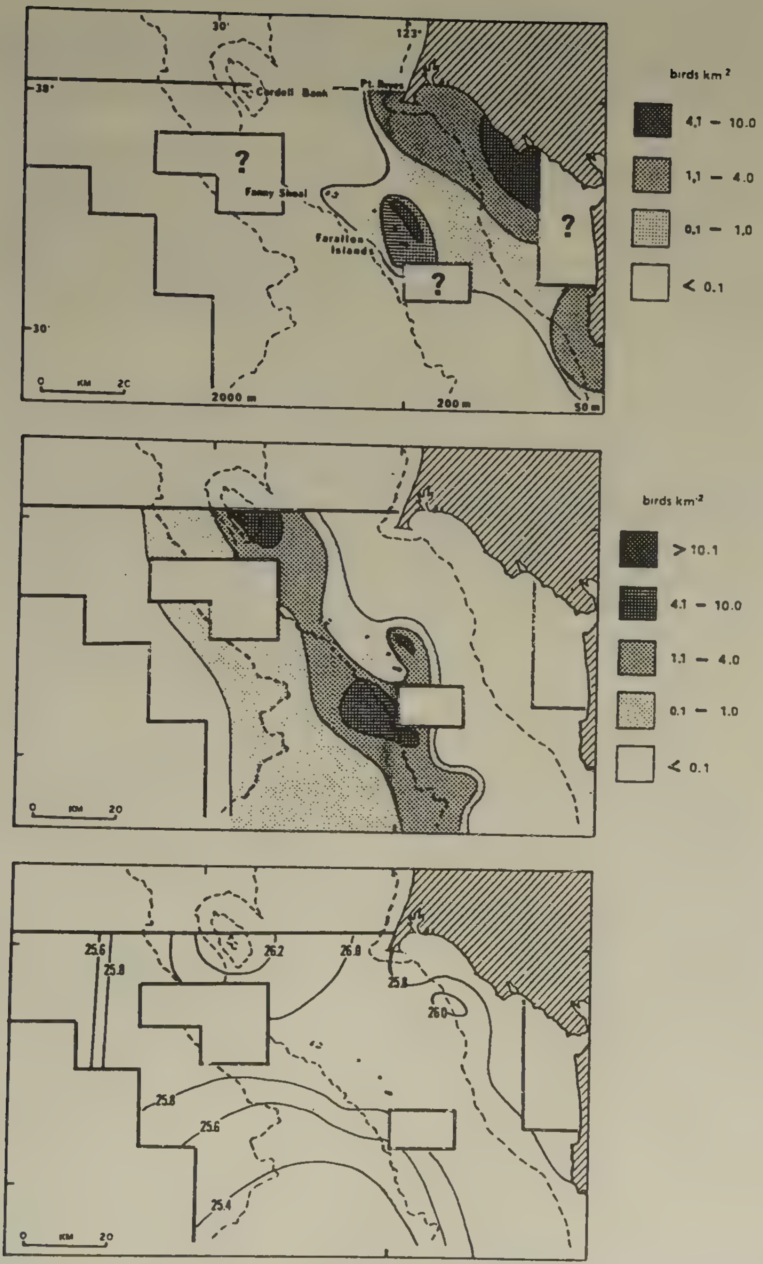
During six cross-shelf aerial surveys in March through May, Common Murres were consistent in distribution relative to mainland and Farallon colonies. Occurring in large numbers to about 20 km from the colony, murre densities correlated negatively with water depth, distance to the mainland, and distance to the Farallones. A feeding area 8–25 km northeast of the islands was occupied by numerous large flocks from mid-April to early June. After that, murres favored waters within 12 km of the colonies on the mainland and Farallones (Fig. 1).

In June, murres occupied waters having a variety of temperature and salinity conditions. They preferred turbid water near colonies, but their abundance was not correlated with water density at 10 m (an index to the recency of upwelling; Fig. 1). A regression model explaining 31% of density variation in murres incorporated optical depth (OD) and distance to the nearest colony (DC):

$$\log \text{density} = -0.02\ \text{OD} - 0.005\ \text{DC} + 0.41 \qquad (1)$$

$$(\text{ANOVA } F_{2,49} = 12.07,\ P < 0.001)$$

Where birds fed near the coast, surface estuarine outflow from San Francisco Bay was underlain by salty, cold water that probably had been upwelled along the outer shelf. Fish such as anchovies (*Engraulis mordax*), smelt (Osmeridae), and small lingcod (*Ophiodon elongatus*) constituted the nearshore diet. From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Pt. Reyes
?
Fanny Shoal
Farallon Islands
?
?
30'
0 KM 20
2000 m
200 m
50 m
birds km⁻²
4.1 – 10.0
1.1 – 4.0
0.1 – 1.0
< 0.1
0 KM 20
birds km⁻²
> 10.1
4.1 – 10.0
1.1 – 4.0
0.1 – 1.0
< 0.1
25.6
25.8
26.2
26.8
25.8
26.0
25.8
25.6
25.4
0 KM 20

**Figure 1.** Distributions of Common Murres (top) and Cassin's Auklets (middle) compared with plot of water density (sigma t) at 10 m (bottom), 12–17 June 1985. Areas not sampled are delimited by double lines.

the Farallones, murres foraged in waters intermediate in character between recent upwellings (cold and salty) and estuarine outflow. Diets on the outer shelf changed after 20 April from almost all euphausiids to almost all juvenile rockfish (Table 1).

From continuous ship-transect data, we determined the variance to mean ratios for bird density in transect intervals ranging from 1 to 64 km (Ord 1972; Schneider and Duffy 1985). At all measurement intervals, density variation in murres was greater in the cross-shelf than the along-shelf direction. Peak variance to mean ratios ($I'$), which we interpret to indicate the scales at which bird aggregation was most intense, occurred at measurement intervals of 8–24 km across the shelf and 16–24 km along the shelf (Fig. 2).

The center of auklet distribution shifted at onset of egg laying in late March from offshore of the continental slope (200–2000 m in depth) toward the shelf break. Auklets were usually abundant north, rather than south, of the colony. In April, May, and early June, auklet density varied inversely with distance from the shelf break and distance from the colony, but did not correlate with depth or distance to the mainland. In late March, as auklets shifted toward the shelf break, they aggregated at shorter spatial scales than in mid-March, when they were widely dispersed off the shelf; the scale of maximum intensity of aggregation in the cross-shelf direction diminished from $I'_{max} = 32$ km to $I'_{max} = 16$ km (Fig. 2). In the along-shelf direction, peak auklet aggregation occurred at 48+ km in all months.

In mid-June, we began to see auklets 15–25 km southwest of the colony. At this time, we encountered no auklets over the inner shelf, large numbers in the edges and core of the cold upwelling filament west of Point Reyes (to 63 km from the colony), and none for 50 km seaward of the filament. Returning southeast toward the colony, we again encountered a few auklets in the core of the filament and many within 20 km of the island, where temperature and salinity characteristics were those of a relict upwelling.

Along the inner edge of the filament and at Fanny Shoal, auklets ate euphausiids (Table 1). Adults of one prey species, *Thysanoessa spinifera*, concentrated at or below the thermocline by day during the nonupwelling season. After the onset of upwelling, surface swarms became frequent. In June 1985, *T. spinifera* was abundant along the outer shelf, avoiding nearshore waters and those seaward of the shelf break. *Euphausia pacifica* inhabited the upper continental slope, where most adults apparently remained below the thermocline until dark. In deep water southwest of the colony, auklets ate mainly small (30 mm) rockfish (*Sebastes* spp.). These offshore surface waters were relatively fresh and warm, and a strong thermocline existed at 15–30 m. A regression model incorporating water density (sigma t) at 10 m, optical depth (OD), and distance to the colony (DC) explained 36% of variation in auklet density:

$$\text{log density} = 0.34 \text{ sigma t} - 0.006 \text{ DC} - 0.06 \text{ OD} - 8.2 \qquad (2)$$

$$(\text{ANOVA } F_{2,49} = 26.22, P < 0.001)$$

In previous years, auklets occurred in large numbers at Cordell Bank (Briggs *et al.* 1983). During 1985, they mostly avoided the area until the upwelling

**Table 1.** Major components of diets of Cassin's Auklets and Common Murres off the central California coast, March–July 1985.[*]

| Bird species | Period | Location[†] | Sample size | No. of prey species | Prey species | % occurrence | % frequency |
|---|---|---|---|---|---|---|---|
| Cassin's Auklet | Late March | FS–CB | 13 | 3 | *Thysanoessa spinifera* | 54 | 15 |
| | | | | | *Euphausia pacifica* | 100 | 85 |
| | Mid-April | NFAR | 5 | 2 | *T. spinifera* | 80 | 12 |
| | | | | | *E. pacifica* | 100 | 88 |
| | Early June | FS–CB | 8 | 4 | *T. spinifera* | 38 | 23 |
| | | | | | *E. pacifica* | 88 | 73 |
| | | | | | *Sebastes* spp. | 50 | 40 |
| | | NFAR | 6 | 4 | *T. spinifera* | 67 | 59 |
| | | | | | *Sebastes* spp. | 83 | 15 |
| | | SFAR | 11 | 8 | *T. spinifera* | 9 | 7 |
| | | | | | *E. pacifica* | 9 | 7 |
| | | | | | *Sebastes* spp. | 73 | 26 |
| | Mid-June | FS–CB | 7 | 4 | *T. spinifera* | 28 | 1 |
| | | | | | *E. pacifica* | 86 | 96 |
| | | | | | *Sebastes* spp. | 86 | 3 |
| | | NFAR | 4 | 3 | *T. spinifera* | 50 | 18 |
| | | | | | *E. pacifica* | 75 | 27 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  |  |  |  | *Sebastes* spp. | 100 | 55 |
|  | Late July | NFAR | 10 | 3 | *T. spinifera* | 70 | 24 |
|  |  |  |  |  | *E. pacifica* | 80 | 75 |
| Common Murre (offshore samples only) | Mid-April | NFAR | 7 | 4 | *T. spinifera* | 71 | 7 |
|  |  |  |  |  | *E. pacifica* | 57 | 92 |
|  |  |  |  |  | *Brachyistius frenatus* | 28 | 1 |
|  |  | SFAR | 5 | 4 | *T. spinifera* | 80 | 85 |
|  |  |  |  |  | *E. pacifica* | 60 | 2 |
|  |  |  |  |  | *Sebastes* spp. | 100 | 13 |
|  | Mid-June | NFAR | 7 | 3 | *E. pacifica* | 14 | 6 |
|  |  |  |  |  | *Sebastes* spp. | 100 | 87 |
|  | Late July | NFAR | 5 | 3 | *Sebastes* spp. | 100 | 99 |

*Only birds containing food are reported.

† Locations: FS-CB: Fanny Shoal to Cordell Bank, 20–35 km northwest of Farallones colony.
NFAR: Near North and Middle Farallones, 6–11 km northwest of Farallones colony.
SFAR: Near South Farallon, 1–15 km west, southeast, or east of Farallones colony.

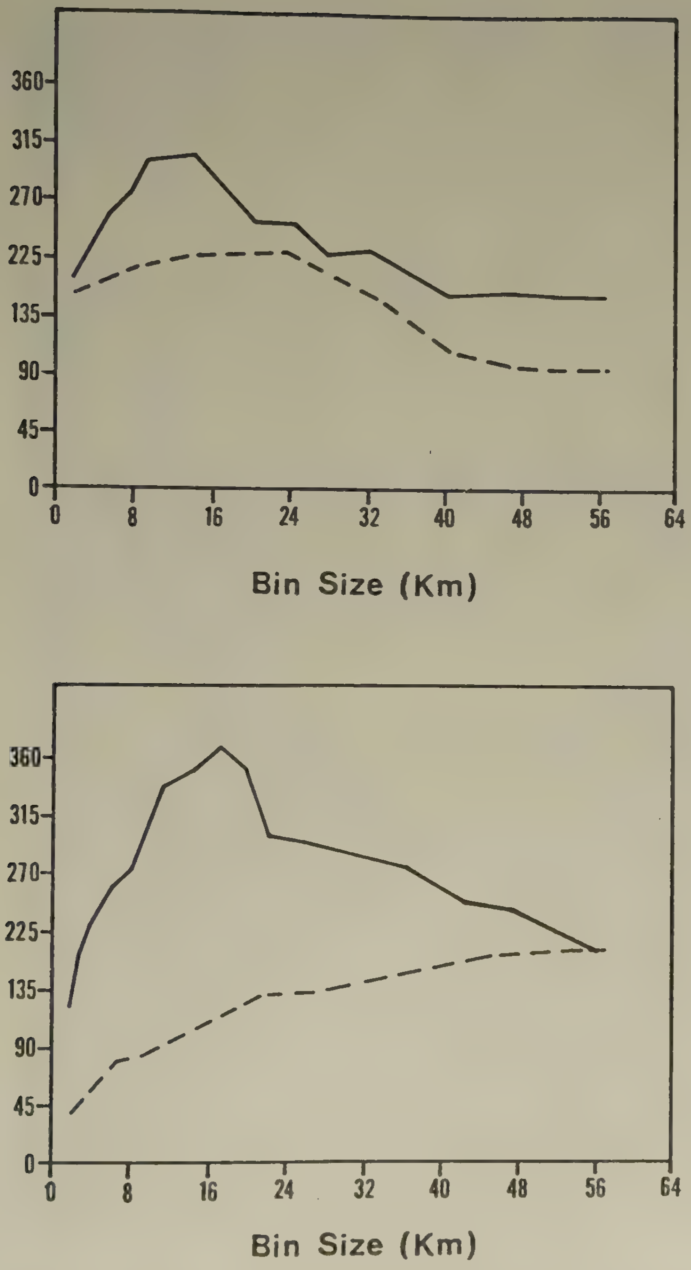

**Figure 2.** Intensity of aggregation (I′ of Ord 1972) as a function of scale of measurement for Common Murres (top) and Cassin's Auklets (bottom) for ship transects, late May to mid-June 1985. Cross-shelf data are shown with solid lines and along-shelf data with dashed lines.

filament appeared with its strong thermal and optical gradients. Analysis of extensive bird surveys and satellite imagery from central California (J.C. Mueller, L.C. Breaker, and KTB, unpublished data) indicated that auklets are abundant primarily in waters having moderate thermal gradients (0.01–0.10°C·km$^{-1}$) and moderate clarity (optical depth narrowly restricted to 7.5–8.3 m). Almost all auklets we observed in June 1985 occurred in waters having an optical depth of 5–7 m.

Many questions about links between physical processes, prey populations, and these seabirds remain unanswered. Depths at which the birds obtain food are not known, nor are the specifics of the vertical distributions or scales of aggregation of the prey. During 1985, juvenile rockfish and *E. pacifica* occupied bands along the shelf break with considerable along-shelf continuity (tens of kilometers). This pattern was matched by the auklet but not the murre. A possible explanation lies in the occurrence of murres in relatively murky coastal water northeast of the Farallones; waters were much clearer along the shelf break. Might the greater escape capabilities of small fish (relative to euphausiids) be offset in murky water, where murres can closely approach prey before being detected (Ainley 1977)? On the other hand, why do auklets frequent relatively clear water? Is this the type of water where detection and capture of euphausiids is easiest? Or is this optical characteristic merely a "tracer" for the kind of habitat having the highest numbers of prey? Detailed sonographic transects might provide an answer.

The distribution of auklets relative to the upwelling filament in mid-June suggests that foraging success is enhanced at the upwelling frontal zone. Auklets concentrated only in newly upwelled water or where the same dense subsurface waters lay beneath a shallow thermocline. Fanny Shoal, where auklets fed for more than two months, was bathed much of the time in recently upwelled water. Studies of satellite archives show that the Farallones / Point Reyes / Cordell Bank is one region where upwelling fronts frequently recur and persist up to several weeks (J.C. Mueller and L.C. Breaker, pers. commun.). Such consistency should allow auklets to track the evolution of these features.

A variety of seabirds now have been shown to concentrate at mesoscale ocean features having large property gradients (e.g., midshelf fronts, ice edges, tidally forced divergences, boundaries of Gulf Stream eddies) (Brown 1980; Ainley and Jacobs 1981; Schneider and Hunt 1982; Haney 1985). Off the California coast and elsewhere, the shelf break and associated upwelling fronts appear to segregate different elements of the seabird community. As interdisciplinary studies of the shelf-break zone go forward, we may find that birds such as auklets are uniquely adapted to exploit this intensely variable environment.

## Acknowledgments

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# AGE-SPECIFIC VULNERABILITY OF PACIFIC SARDINE, *SARDINOPS SAGAX*, LARVAE TO PREDATION BY NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

To a large degree interannual variability in recruitment determines the size of pelagic fish populations. Recruitment to the Pacific sardine, *Sardinops sagax*, population off California varies from year to year over several orders of magnitude and is unrelated to spawning stock size (Murphy 1966; MacCall 1979). Variable mortality rates in the first year of life must determine year-class strength, although the sources of this variability are unknown. Mortality rates in the earliest stages are size specific with highest rates in the egg and yolk-sac stage (Ahlstrom 1954; Butler 1987) and may contribute to variability in year-class strength (Smith 1985).

The sources of mortality of sardine larvae have yet to be investigated. In other pelagic larvae, mortality is due to either starvation or predation, and starvation is significant only during the brief period after the onset of feeding (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986; Owen et al. 1987). In sardines, significant mortality occurs during the egg and yolk-sac stages (Ahlstrom 1954) and this mortality can only be due to predation. Variable mortality in older larval and juvenile sardines may also contribute to variability in recruitment, and this mortality, as in other fishes, may also be due to predation (Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of Pacfiic sardine larvae to predation by adult northern anchovies, *Engraulis mordax*. The vulnerability of cape anchovy and northern anchovy larvae to cannibalism has been investigated by Brownell (1985) and Folkvord and Hunter (1986) and found to be an important source of mortality. In this paper the vulnerability of sardine larvae will be compared with that of anchovy larvae and differences in the biology of sardines and anchovies will be discussed.

Our approach was to observe the avoidance behavior of Pacific sardine larvae in response to predatory attacks by northern anchovy adults. Adult northern anchovy were chosen as a predator because the northern anchovy was the most abundant pelagic fish in the California Current region during the waning years of the sardine fishery and because its planktivorous diet includes fish eggs and larvae (Loukashkin 1970; Hunter and Kimbrell 1980).

## Materials and Methods

### Experimental Fishes

The Pacific sardine larvae used in the experiments were reared from eggs spawned in the laboratory. Adult Pacific sardines were collected off San Diego and held in 175 $m^3$ aquarium for six months. Males and females with developing gonads were isolated in spawning tanks and injected with 250 mg human chorionic gonadotropin and on the following day injected with 200 units pregnant mare serum and 20 mg salmon pituitary extract. On the third day fertilized eggs were collected from the spawning tank. Larval rearing procedures follow those described by Hunter (1976). Temperature in the rearing tanks was maintained at 21°C.

### Apparatus and Procedures

Experimental apparatus and procedures were the same as those described by Folkvord and Hunter (1986) but will be briefly outlined here. Experimental predators were two groups of 5 adult northern anchovy (range of standard lengths 8.4–9.2 cm). Predators were maintained in two rectangular fiberglass tanks ($0.75 \times 2.15 \times 0.83$ m = 1.35 $m^3$) and fed adult brine shrimp except on days of experimental observation. Seawater was supplied continuously to the tanks except during experiments. The temperature in the observation tank ranged from 16.2° to 22.8°C (mean = 20.1°C). Two 100 W incandescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosing a window on one side of the tank provided a darkened observation chamber.

Each trial consisted of the encounter of three prey with the predators. Prey were introduced into the observation tank with a clear glass beaker. Initial feeding behavior of the predators is quite variable but becomes less variable as the predators become accustomed to prey in the tank. For this reason, prior to each experiment adult *Artemia* were introduced as prey for five consecutive trials to standardize predator behavior. After the preliminary trials with *Artemia*, three trials with sardine larvae were alternated with one trial with brine shrimp until 18 trials with sardine larvae were completed. Each experiment was concluded with a trial of brine shrimp to test for satiation.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. The mean standard length was determined from 20 larvae sampled randomly from the rearing tank on the day of each behavior experiment. The numbers of observations for each size class (mean SL) were 8.0 mm, 41; 11.3 mm, 51; 12.1 mm, 114; 12.7 mm, 46; 14.1 mm, 81; 17.6 mm, 104; and 19.6 mm, 69. Experiments were not extended to larger sizes due to insufficient numbers of larvae.

### Classification of Behavior

Prey behavior was scored only when the predator attacked a prey. Four measures of predator-prey interactions were calculated: predator attack distance, the distance from which the predator responded to the prey and initiated its attack; frequency of avoidance response; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). An avoidance response was a change in speed or trajectory of a larvae before the predator had completed its attack by closing its mouth. An escape was defined as a larval response in which the predator failed to capture the larvae in a single attack. Typically adult anchovy make a single attack on a prey item and do not pursue a prey that escapes (Folkvord and Hunter 1986) but rather continue searching the tank. Thus attacks on one prey item were recorded twice if the first attack was unsuccessful. Although predator attack distance was recorded, this measurement is highly subjective and comparison with the measurements of other observers is suspect. We did not analyze predator attack distance for this reason.

To compare response and escape behaviors of Pacific sardine with those reported by Folkvord and Hunter (1986) for northern anchovy at similar stages of development, mean lengths were converted to ages using field growth rates back-calculated from otolith increment widths for each species. Confidence limits of the percentage of larvae responding or escaping attack were estimated assuming the binomial distribution.

## Results

### Probability of Response to Attack

The youngest larval stages of both sardine and anchovy were the most vulnerable to predation. Only 17% of 8 mm sardine larvae (smallest size tested) responded to attack by adult anchovy. With increasing size more sardine larvae responded to attack. At 20 mm, the largest size tested, 61% of the larvae responded to attack. The response rate of Pacific sardine larvae was consistently lower than that of northern anchovy larvae of similar lengths (Fig. 1). Although this difference in responsiveness could be due to differences in the observer, it may also be explained by the difference in age of anchovy and sardine at the same length. Sardine larvae are about 6.2 mm when they begin feeding (age = 5 days from fertilization at 17°C), whereas first-feeding anchovy larvae are only about 4.3 mm (age = 5 days from fertilization at 17°C) (Zweifel and Lasker 1976). Sardine larvae also grow faster than anchovy larvae at the same temperature (Butler and Rojas de Mendiola 1985). Thus, sardine larvae are younger at a given size than anchovy larvae.

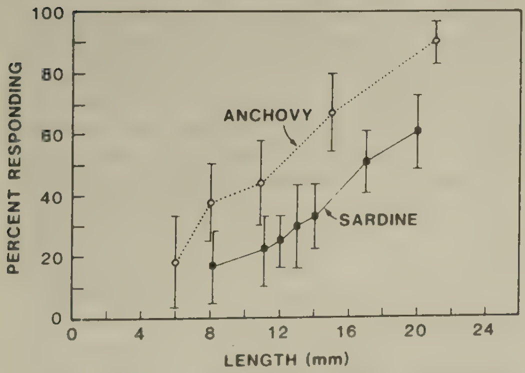

FIGURE 1.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

Since the latency of response to attack must be related to the development of the central nervous system (Webb 1981; Webb and Corolla 1981), it may be more appropriate to compare sardine larvae with anchovy larvae of the same age. For that reason lengths of the larvae of both species were converted to age using growth rates measured in the field (Methot and Kramer 1979; Butler 1987). Comparison of the percentage of larvae responding to attack at a given age (Fig. 2) reveals no significant difference in the rate of development of response to attack. Thus, the escape response develops at the same rate in Pacific sardine and northern anchovy, and the difference in proportion of larvae responding at a given size (Fig. 1) is due to the difference of size at hatching and the difference in growth rates of the two species.

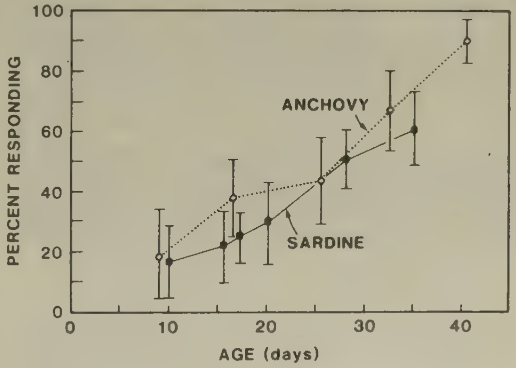

FIGURE 2.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

### Probability of Escaping Attack

The ability to successfully avoid attack increased with size of Pacific sardine as well as northern anchovy. Few small larvae of either specie escaped attack by adult northern anchovy. Only 3% of 8 mm sardine larvae escaped attack and the percentage of larvae escaping increased to only 11% for 17 mm larvae and 13% for 20 mm larvae (Fig. 3). The proportion of small anchovy larvae escaping attack was also low (6%) but increased with size to 73% of 22 mm larvae (Folkvord and Hunter 1986). The numbers of larvae escaping attack were significantly different between anchovy and sardines at sizes larger than about 13 mm. Conversion of lengths to age using field growth rates does not eliminate the differences between sardine and anchovy (Fig. 4). Sardine larvae older than 20 days were more vulnerable to predation than anchovy larvae of the same age (Fig. 4).

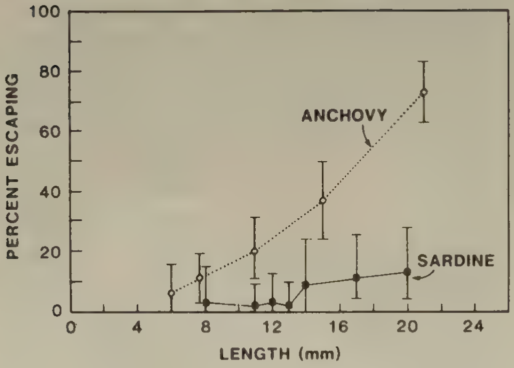

FIGURE 3.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

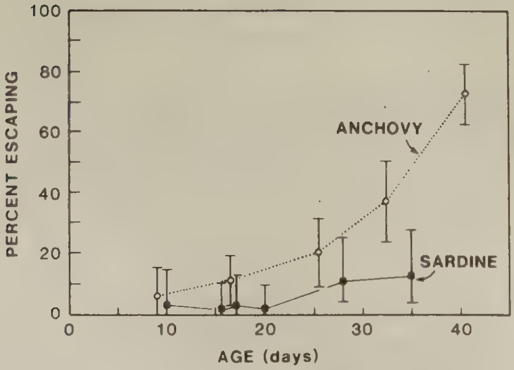

FIGURE 4.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

## Discussion

The proportion of Pacific sardine larvae responding to attack and escaping attack increased with size and with age. Our results differ from those reported by Folkvord and Hunter (1986) for anchovy larvae in the rate at which sardine larvae respond and escape attacks at given sizes and ages. It should be noted that, although the methodology was the same, the observers were different. This difference could affect rate of response to attack. It also should be noted that the size of adult anchovy used by Folkvord and Hunter (1986) ranged from 83 to 89 mm SL, whereas the size range was 84–95 mm SL in our study and that the size of predator influences the number of larvae escaping (Folkvord and Hunter 1986). The slightly larger size of predators used in this study is not sufficient to explain difference in escapement, nor is the difference in observer likely to affect the rate of escapement since the observer's task is to examine whether the larvae are escaping or are being eaten.

The greater vulnerability to predation of sardine larvae than anchovy larvae has interesting implications. In general, larger larvae are less vulnerable to predation than small larvae. Bailey (1984) and Bailey and Batty (1983) compared the vulnerability of cod, flounder, plaice, and herring larvae to predation by invertebrate predators. They found that herring larvae were the least vulnerable larvae because herring were more reactive and had the greatest escape speeds. Sardine larvae are larger at hatching and at a given age are larger than anchovy larvae. In our experiment sardine larvae react to predatory attacks at similar rates as anchovy larvae, but escape attack at a much lower rate.

This difference in vulnerability to attack may be due to differences in swimming behavior. Anchovy larvae swim using beat and glide locomotion (Hunter 1972). The escape behavior is usually a burst of swimming from a motionless position (Folkvord and Hunter 1986). We observed that sardine larvae, however, swim continuously and they respond to attack by changing direction and increasing speed. This difference in swimming mode may affect escape behavior in two ways. The escape behavior of sardine larvae may be less flexible than that of anchovy larvae because the direction the sardine larvae takes is largely determined by its trajectory. Since sardine larvae cruise, their scope for activity (escape behavior) may be limited. Anchovy larvae accelerate from a standing start and have the possibility of moving in a number of directions. We speculate that the beat and glide behavior of anchovy larvae may not only be hydrodynamically more efficient (Weihs 1974) but also may reduce the vulnerability to predation.

## Acknowledgments

Roderick Leong maintained sardines in the laboratory and spawned the adults after manipulation with hormones. Sandor Kaupp reared sardine larvae in the laboratory. Arild Folkvord and Clelia Booman elaborated experimental procedures. John R. Hunter commented on the manuscript.

## Literature Cited

AHLSTROM, E. H.
1954. Distribution and abundance of egg and larval populations of the Pacific sardine. Fish. Bull., U.S. 56:83–140.

BAILEY, K. M.
1984. Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. Mar. Biol. (Berl.) 79:303–309.

BAILEY, K. M., AND R. S. BATTY.
1983. A laboratory study of predation on *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. Mar. Biol. (Berl.) 72:295–301.

BROWNELL, C. L.
1985. Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. Trans Am. Fish. Soc. 114:512–518.

BUTLER, J. L.
1987. Comparisons of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph.D Thesis, University of California at San Diego, San Diego, 242 p.

BUTLER, J. L., AND B. ROJAS DE MENDIOLA.
1985. Growth of larval sardines off Peru. CalCOFI Rep. XXVI:113–118.

FOLKVORD, A., AND J. R. HUNTER.
1986. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes. Fish. Bull., U.S. 84:859–869.

HEWITT, R. P., G. H. THEILACKER, AND N. C. H. LO.
1985. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26:1–10.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821–838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81–88.
1984. Inferences regarding predation on the early life stages of cod and other fishes. Flodevigen rapportser., 1., ISSN 0333-2594 The propagation of cod *Gadus morhua* L, p. 533-562.

HUNTER, J. R., AND C. A. KIMBRELL.
1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 78:811–816.

LOUKASHKIN, A. S.
1970. On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). Proc. Calif. Acad. Sci. 37 (Ser. 4):419–458.

MACCALL, A. E.
1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. 10:72–82.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413–423.

MURPHY, G. I.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. 34:1–34.

O'CONNELL, C. P.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475–484.

OWEN, R. W., J. L. BUTLER, N. C. H. LO, A. ALVARINO, G. H. THEILACKER, J. R. HUNTER, J. HAKANSON, AND Y. WATANABE.
In press. Spawning and survival patterns of larval anchovy in contrasting environments—a site intensive experiment. Cal. Coop. Fish. Invest. Rep.

SMITH, P. E.
1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):69–82.

THEILACKER, G. H.
1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull., U.S. 84:1–15.

WEBB, P. W.
1981. Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivor, *Amphiprion percula*. Fish. Bull., U.S. 79:727–735.

WEBB, P. W., AND R. T. COROLLA.
1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 79:143–150.

WEBB, P. W., AND D. WEIHS.
1986. Functional locomotor morphology of early life history stages of fishes. Trans. Am. Fish. Soc. 115:127.

WEIHS, D.
1974. Energetic advantages of burst swimming of fish. J. Theoret. Biol. 48:215–229.

ZWEIFEL, J. E., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609–621.

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# TROPHIC RELATIONSHIPS OF THE SHORTBELLY ROCKFISH, *SEBASTES JORDANI*, OFF CENTRAL CALIFORNIA

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## ABSTRACT

The shortbelly rockfish, *Sebastes jordani*, the most numerous species of *Sebastes* off central California, feeds primarily on *Euphausia pacifica* and other euphasiids. This rockfish forages in the water column at night, and even more intensively near the bottom during the day. Its major prey, *E. pacifica*, normally inhabits deeper water outside the shelf, where it occurs at depths of 200–400 m during the day. At night, however, *E. Pacifica* migrates upward in the water column, and many are transported over the shelf by prevailing currents. In the morning, when they attempt to descend to their normal daytime depths, many become trapped on the relatively shallow shelf, where *S. jordani* probably find these organisms especially vulnerable.

## RESUMEN

*Sebastes jordani*, la especie más numerosa de *Sebastes* en la costa central de California, se alimenta principalmente de *Euphausia pacifica* y otros eufáusidos. Este pez se alimenta en la columna de agua durante la noche, y más intensamente cerca del fondo durante el día. Su presa principal, *E. pacifica*, vive normalmente en aguas profundas fuera de la plataforma continental, en profundidades de 200 a 400 m durante el día. Sin embargo, durante la noche, *E. pacifica* migra hacia la superficie donde numerosos individuos son transportados hacia la costa por las corrientes predominantes. En la mañana, cuando estos organismos intentan completar su migración hacia las profundidades diurnas normales, se encuentran atrapados en las aguas costeras menos profundas donde son particularmente vulnerables a la predación por *S. jordani*.

## INTRODUCTION

The shortbelly rockfish, *Sebastes jordani*, a potentially rich but unfished resource off California (Lenarz 1980), occurs on the continental shelf from northern Baja California, Mexico (lat. 31°N), to Vancouver, British Columbia, Canada (50°N). It is most numerous off central California, where its biomass between San Francisco and Monterey has been estimated to be 295,000 metric tons—more than 10 times the estimated combined biomass of all other species of *Sebastes* within that area (Gunderson and Sample 1980). The adults of this relatively small scorpaenid (to about 32 cm TL) occur at depths from about 90 to 280 m (Miller and Lea 1972).

In making tentative management recommendations, Lenarz (1980) cautioned that the trophic relationships of this species should be better understood before its exploitation is permitted. The shortbelly is an important prey of chinook salmon, *Oncorhynchus tshawytscha* (Merkel 1957), and current study at the National Marine Fisheries Service Tiburon Laboratory has shown that it is also seasonally important to other coastal predators, including coho salmon (*Oncorhynchus kisutch*) (P.A. Adams, Tiburon Laboratory, pers. comm. Jan. 1983); lingcod (*Ophiodon elongatus*); and black rockfish (*Sebastes melanops*) (E. S. Hobson, J. R. Chess, and D. F. Howard, Tiburon Laboratory, unpubl. data 1985). Little is known about its predatory habits, however, beyond the report that adults feed exclusively on macrozooplankton, primarily euphausiids (Phillips 1964).

Here we describe the diel feeding pattern of the shortbelly relative to variations in the availability of potential prey. We then discuss how the shortbelly's distribution on the coastal shelf off central California is influenced by mechanisms affecting the distribution of its prey.

## METHODS

### *Study Area*

This study is based on collections and observations made during 10 cruises involving 74 days at sea between 1979 and 1982. Exploratory surveys during November 1979 and March 1980 used hydroacoustics and trawls to locate concentrations of shortbellies in the area between Point Sur (36°18′N) and Point Reyes (38°4′N). These explo-

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TABLE 1
**Areas Trawled during Each Cruise, Showing Number of Positive *S. jordani* Catches/Total Number of Trawl Sets Taken**

| | Month/year of cruises | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 11/79 | 3/80 | 7/80 | 11/80 | 3/81 | 5/81 | 9/81 | 1/82 | 3/82 | 9/82 | 11/82 |
| Pescadero Point | 7/14 | 4/7 | 2/6 | 0/3 | — | 2/5 | 0/4 | 0/1 | — | — | — |
| Ascension Canyon | 3/6 | — | 2/3 | 5/12 | 2/4 | 0/5 | 4/11 | 4/7 | 3/8 | 4/11 | 0/6 |
| Monterey | — | 2/4 | — | — | — | 0/2 | — | — | — | — | — |
| Point Sur | — | 2/4 | — | — | 2/2 | 0/1 | — | — | — | — | — |

rations found the species concentrated where the coastal shelf extended offshore, often near submarine canyons (the same areas where Gunderson and Sample [1980] had found them abundant during a 1977 coastwide rockfish survey). They were most numerous at depths between 120 and 240 m along about 40 km of the coastal shelf's outer edge offshore of Pescadero Point (at approximately 37°13′N), and the areas immediately north of Ascension and Sur canyons (Figure 1 and Table 1). Work was concentrated at these locations following the exploratory cruises of 1979 and 1980, but exploratory surveys were continued elsewhere as opportunities arose. Although these additional surveys located small concentrations at other places, usually on the outer shelf, the more than 340 hours of additional hydroacoustic search and exploratory trawling between Point Sur and Point Reyes failed to locate concentrations that matched those in the primary study areas defined above.

### *Collections*

The collections were scheduled to define diel and geographical patterns in trophic relationships. The diel feeding patterns discussed below are based on stomach contents of shortbellies trawled from the Ascension area during the hours immediately before sunset and sunrise—times that have been found most effective in defining diel feeding patterns of predatory fish (e.g., Hobson 1974; Hobson and Chess 1976). The geographical patterns are based on shortbellies collected at the various stations during all periods of the diel cycle. Scheduled plankton collections were made during midday (1100–1400 h) and midnight (2200–0100 h) at the Ascension area to define diel variations in prey abundance and distribution.

Shortbellies were collected with a three-bridle midwater trawl that had 30.5-m headropes and footropes. We used a Furuno MkII net monitor with an acoustic link to position the trawl at the depths of the strongest acoustic targets. Often, however, the trawl followed a course offset from that of the ship (due either to the effects of subsurface currents on the trawl, or winds on the ship), which hampered attempts to position the trawl on specific acoustic targets located by shipboard echo sounders. Most sets were made on aggregations that had been located hydroacoustically, but blind sets made where we had found shortbellies earlier were often successful even in the absence of acoustic targets. The standard trawling duration was 20 minutes, but the net was retrieved sooner if there were indications (hydroacoustic or otherwise) that it had passed through a large aggregation of fish. Each catch, or a portion of the catch, was grossly subdivided by size, and from each size group 10 fish were retained for stomach-content analysis. (Fish with any evidence of everted stomachs, an unusual condition, were not included.) A total of 977 specimens were measured (standard length). Their stomachs were removed and preserved, and the contents were analyzed later in the laboratory.

Zooplankton were collected with a messenger-activated, opening-closing 1-m$^2$ Tucker trawl (Hopkins et al. 1973) fitted with two 0.335-mm mesh nets. Because the net frame was inclined 45° while fishing, its 1 × 1.4-m opening was in effect reduced to 1 m$^2$. A total of 84 plankton samples stratified by depth were taken during seven cruises. Each cruise included a series of three plankton collections made on two successive days and nights ($n = 12$). The three collections of each series were replicated at estimated depths of 18, 55, and 119 m along the 137-m (75-fm) isobath. (The ship sometimes drifted off course over depths that varied from about 128 to 145 m.) Sampling depths were determined by wire angle and length, and were standardized by maintaining the wire at 45° (which required a speed of approximately 127 cm $^{\text{sec-1}}$) for the 15-minute collection periods. Four test runs using digital flowmeters indicated that this procedure filtered about 1,114 m$^3$ of water. We used elapsed time and wire angle, rather than a flowmeter, to standardize our samples.

For later analysis in the laboratory, a measured proportion, usually about a 500-ml aliquot of each collection (settled volume) was preserved in 4% buffered formaldehyde. (The entire collection was preserved if smaller than 500 ml.)

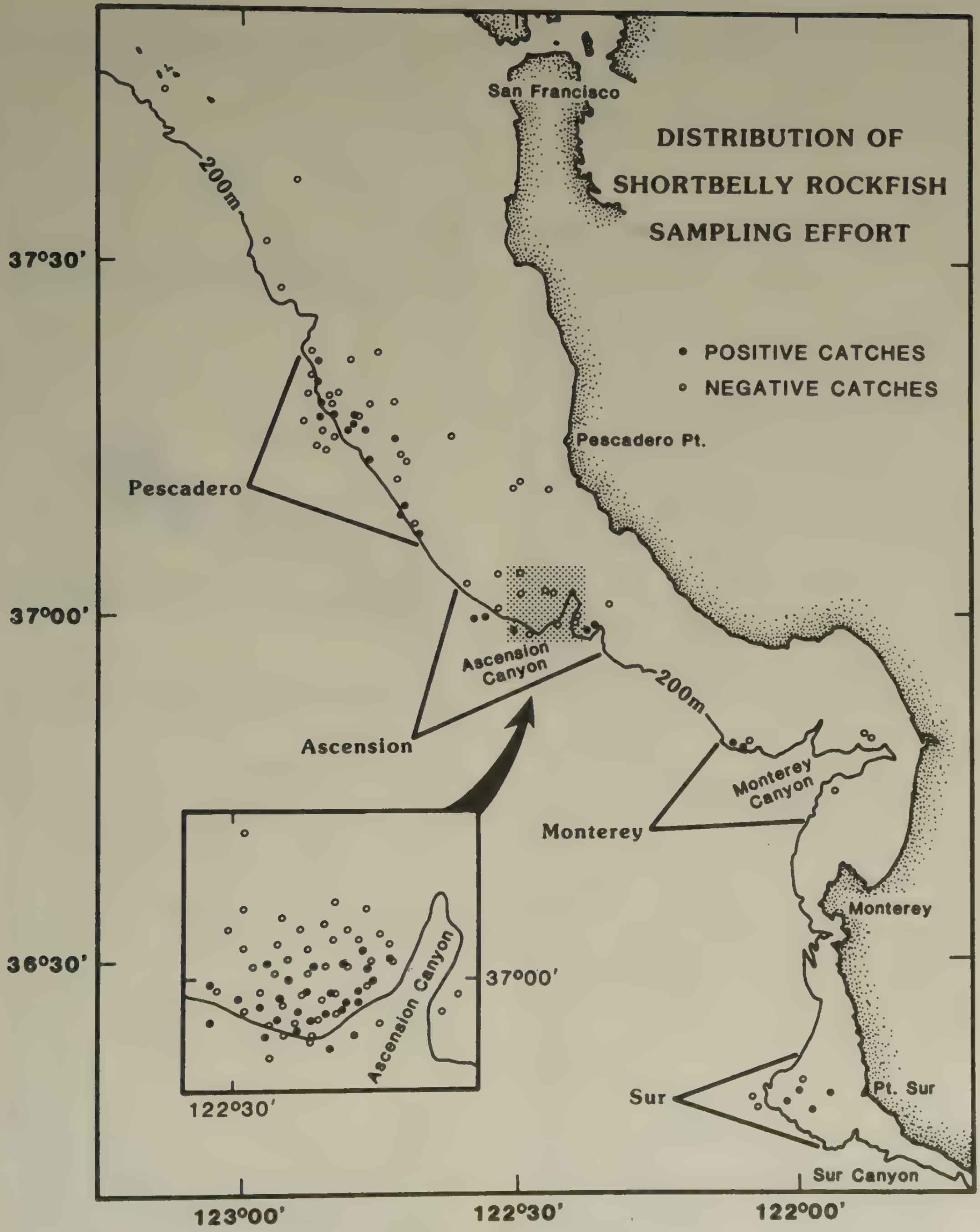
DISTRIBUTION OF
SHORTBELLY ROCKFISH
SAMPLING EFFORT
● POSITIVE CATCHES
○ NEGATIVE CATCHES
San Francisco
200m
Pescadero Pt.
Pescadero
Ascension Canyon
Ascension
200m
Monterey Canyon
Monterey
Monterey
Sur
Pt. Sur
Sur Canyon
37°30'
37°00'
36°30'
123°00'
122°30'
122°00'
Ascension Canyon
37°00'
122°30'

Figure 1. Distribution of shortbelly rockfish sampling effort, giving locations of positive (●) and negative (○) catches.

Additional plankton samples were taken to determine the horizontal distribution of zooplankton within the Ascension study area. These were oblique hauls taken with the Tucker trawl from a depth of 106 m to the surface at specific distances from the canyon. A more complete description of this sample series is presented below.

### *Laboratory Procedures*

In the laboratory, food items from the stomachs were identified to the lowest taxon feasible. For each taxon the following was noted: number, size range, extent of digestion (on a scale of one to five, with one being fresh), and an estimated proportion of the total volume of stomach contents that it represented. An estimate of fullness also was made, although probably this was of questionable value owing to the elasticity of the stomach.

The settled volumes of the preserved plankton aliquots were again determined after the large gelatinous forms had been removed, and workable aliquots of 7–10 ml (settled volume) were obtained with a Folsom plankton splitter. The remainder of each sample was then searched for taxa absent from the aliquoted portion, and these were included in the analysis. For each taxon the following was noted: abundance, estimated volumetric proportion of total sample, and the range of sizes represented. The numbers of organisms in the aliquots were extrapolated to represent the entire sample.

## RESULTS

### *Distribution of* Sebastes jordani

Of 126 trawl sets made at depths from 70 to 275 m between Point Sur and Point Reyes, 48 (38.1%) caught shortbellies. Most of the successful sets were near the outer margin of the shelf at depths of about 150 m, on the north sides of submarine canyons (Figure 1).

During the day, shortbellies were found near the bottom in dense aggregations that often extended 15 m and more into the water column (Figure 2, upper). At night, however, they were more dispersed—20 to 70 m above the bottom—but still 30 m or more below the water's surface (Figure 2, lower). Consistent with this pattern of nocturnal dispersion, our catches after dark took shortbellies more frequently, but in smaller numbers than during the day. At the Ascension Canyon site, for example, 14 (64%) of 22 nocturnal hauls took $\bar{x}$ = 122.9 kg (SE 58.2) of *S. jordani*, whereas 10 (30%) of 33 diurnal hauls took $\bar{x}$ = 1,904.0 kg (SE 687.5).

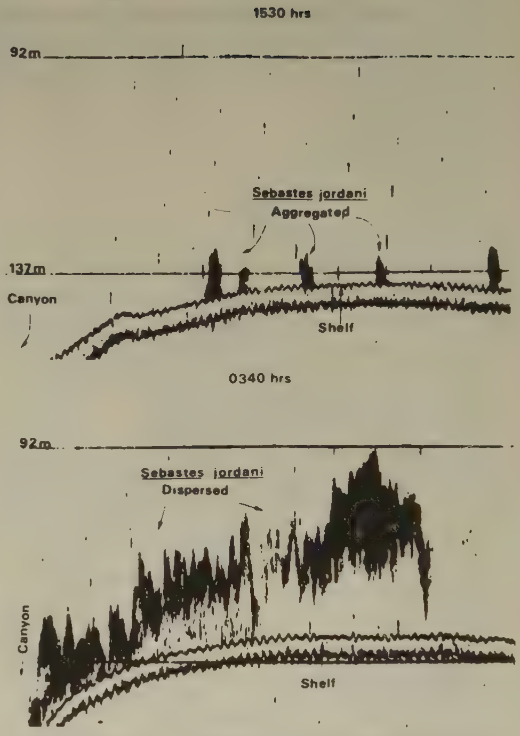

Figure 2. Distribution of shortbellies in the water column during the day (*upper*) and night (*lower*) on the shelf adjacent to Ascension Canyon, January 1982

### *Diet of* Sebastes jordani

Of the 977 shortbellies (99–272 mm SL, $\bar{x}$ = 175 mm) collected for gut analysis (under the wide variety of circumstances sampled during this study), 694 (71%) contained food. Although 87 prey taxa were consumed, only 24 of them occurred in 14 or more (≥ 2%) of the shortbellies examined (Table 2). The primary prey species was *Euphausia pacifica*, but another euphausiid, *Thysanoessa spinifera*, was also important. Most of the prey were relatively large: 68% of the items exceeded 10 mm, and only 7.7% were less than 2 mm (this fact reflected the prominence of euphasiids in the diet). Some minor items, however, were as small as 0.5 mm (e.g., fish eggs). The size and species composition of prey taken by any given shortbelly was influenced by that fish's size. Although the relative importance of euphausiids was greater in larger fish (Table 3), euphausiids and calanoid copepods were the first- and second-ranked prey in all size groups examined.

TABLE 2

**Important Prey of *Sebastes jordani*: Taxa Occurring in at Least 2% of the Stomachs That Contained Food**

| Prey taxa | Freq. occurr. | $\bar{x}$ *n* stom. | Mean % volume | Size range (mm) |
|---|---|---|---|---|
| Polychaeta | | | | |
| *Tomopteris* spp. | .02 | 0.08 | 0.385 | 7.0–15.0 |
| Ostracoda | | | | |
| Halocypridae | .07 | 0.14 | 0.281 | 1.5–4.0 |
| Calanoida | | | | |
| *Calanus pacificus* | .25 | 1.79 | 1.590 | 2.1–2.8 |
| *Candacia bipinnata* | .03 | 0.06 | 0.072 | 2.5–4.0 |
| *Candacia* spp. | .02 | 0.02 | 0.062 | 2.8–4.0 |
| Eucalanidae | .05 | 1.14 | 1.050 | 3.0–9.0 |
| *Eucalanus californicus* | .06 | 0.24 | 0.704 | 3.5–7.0 |
| *Euchirella rostrata* | .12 | 0.55 | 0.859 | 2.3–5.0 |
| *Metridia pacifica* | .17 | 6.17 | 2.091 | 1.4–3.5 |
| *Pleuromamma abdominalis* | .04 | 0.09 | 0.084 | 3.0–4.5 |
| *Pleuromamma* spp. | .14 | 0.65 | 0.899 | 1.5–4.5 |
| *Rhincalanus nasutus* | .08 | 0.36 | 0.555 | 1.4–7.0 |
| *Undeuchaeta bispinosa* | .02 | 0.03 | 0.157 | 4.0–6.0 |
| Undetermined | .20 | 1.28 | 3.165 | 0.9–6.3 |
| Hyperiidea | | | | |
| *Paraphronima* spp. | .02 | 0.04 | 0.196 | 5.0–12.5 |
| Hyperiidae | .04 | 0.12 | 0.050 | 4.0–5.5 |
| Undetermined | .06 | 0.09 | 0.768 | 1.0–15.0 |
| Euphausiacea | | | | |
| *Euphausia pacifica* | .49 | 10.48 | 25.228 | 10.0–24.0 |
| *Nematoscelis difficilis* | .05 | 0.34 | 1.284 | 6.0–22.0 |
| *Nyctiphanes simplex* | .07 | 0.22 | 0.845 | 7.0–19.0 |
| *Thysanoessa spinifera* | .25 | 4.15 | 11.821 | 8.0–29.0 |
| Fragments (digested) | .71 | — | 36.923 | 9.0–23.0 |
| Chaetognatha | | | | |
| Undetermined | .02 | 0.08 | 0.034 | 2.0–25.0 |
| Other | | | | |
| Undetermined digested material | .14 | — | 4.13 | — |

TABLE 3

**Dietary Proportions of Euphausiacea and Calanoida in Three Size Groups of *Sebastes jordani***

| | Mean % diet volume | | |
|---|---|---|---|
| Size of fish (mm) | Euphausiacea | Calanoida | Other |
| 99–160 (*n* = 305) | 68.5 | 17.2 | 14.3 |
| 161–200 (*n* = 199) | 78.6 | 10.5 | 10.9 |
| 201–272 (*n* = 190) | 86.3 | 4.5 | 9.2 |

The shortbellies fed during both day and night. This was demonstrated by fresh prey in gut content samples taken late in the day and shortly before dawn. The 182 individuals (112–261 mm SL, $\bar{x}$ = 167 mm) examined from among those collected at the Ascension Canyon site during the three hours immediately before sunset had consumed $\bar{x}$ = 37.8 prey of $\bar{x}$ = 4.6 taxa, whereas the 237 fish (99–253 mm SL, $\bar{x}$ = 155 mm) collected in the same area during the three hours immediately before sunrise had consumed $\bar{x}$ = 10.2 prey of $\bar{x}$ = 2.1 taxa. Numbers of prey and numbers of taxa are both significantly different (t-test—$\bar{x}$ no. prey: $P \leq 0.01$; $\bar{x}$ no. taxa: $P \leq 0.01$). The incidence of empty stomachs was consistent with these data, because only 12.1% of the day feeders were empty, compared to 26.6% of the night feeders (2 × 2 contingency table, $x^2$ = 12.4, 11 df, $P = 0.005$). Stomach fullness showed the same pattern: the mean fullness of the day feeders was 35.6% (means of individual estimated percent), whereas the night feeders were 28.4% full (Wilcoxon sign rank test, $z = 2.58$, $P \leq 0.001$). Thus although feeding occurred during both day and night, it was more intensive by day.

In relating diel feeding patterns of shortbellies to available prey organisms in the environment, we limited our list of prey taxa to those that occurred in at least 5% of the stomachs examined. We determined that each of these taxa was taken in numbers that differed between day and night (Table 4). While the primary prey, *Euphausia pacifica*, was most numerous in fish collected during the day, two other euphausiids—*Thysanoessa spinifera* and *Nyctiphanes simplex*—were most numerous in fish collected at night.

TABLE 4

**Diel Variations in the Major Prey Taxa* in Stomachs of *Sebastes jordani* Collected at the Ascension Study Area within the 3 Hours Preceding Sunset and Sunrise**

| | Day (*N* = 158) | | | Night (*N* = 174) | | |
|---|---|---|---|---|---|---|
| Major prey taxa | Freq. occurr. | $\bar{x}$ *n* stom. | Mean % diet vol. | Freq. occurr. | $\bar{x}$ *n* stom. | Mean % diet vol. |
| Halocyprid ostracods | .17 | 0.39 | 0.93 | .01 | 0.02 | 0.02 |
| *Calanus pacificus* | .33 | 2.61 | 3.17 | .14 | 1.42 | 1.38 |
| *Eucalanus californicus* | .16 | 0.66 | 2.18 | .01 | 0.01 | 0.01 |
| *Euchirella* spp. | .22 | 1.27 | 3.06 | — | — | — |
| *Metridia pacifica* | .30 | 3.61 | 2.19 | .04 | 0.06 | 0.04 |
| *Pleuromamma* spp. | .32 | 0.85 | 1.03 | .01 | 0.02 | 1.05 |
| *Rhincalanus nasutus* | .15 | 0.94 | 1.11 | .03 | 0.03 | 0.63 |
| *Euphausia pacifica* | .54 | 18.43 | 27.24 | .39 | 2.90 | 19.16 |
| *Nyctiphanes simplex* | .09 | 0.13 | 0.64 | .06 | 0.33 | 1.20 |
| *Thysanoessa spinifera* | .14 | 0.47 | 1.85 | .21 | 2.97 | 11.22 |
| Other Euphausiacea | .04 | 0.05 | 0.36 | .04 | 0.44 | 1.30 |
| Euphausiacea (digested) | .83 | — | 37.78 | .75 | — | 47.67 |

*Taxa that occurred in ≥ 5% of all stomachs examined.

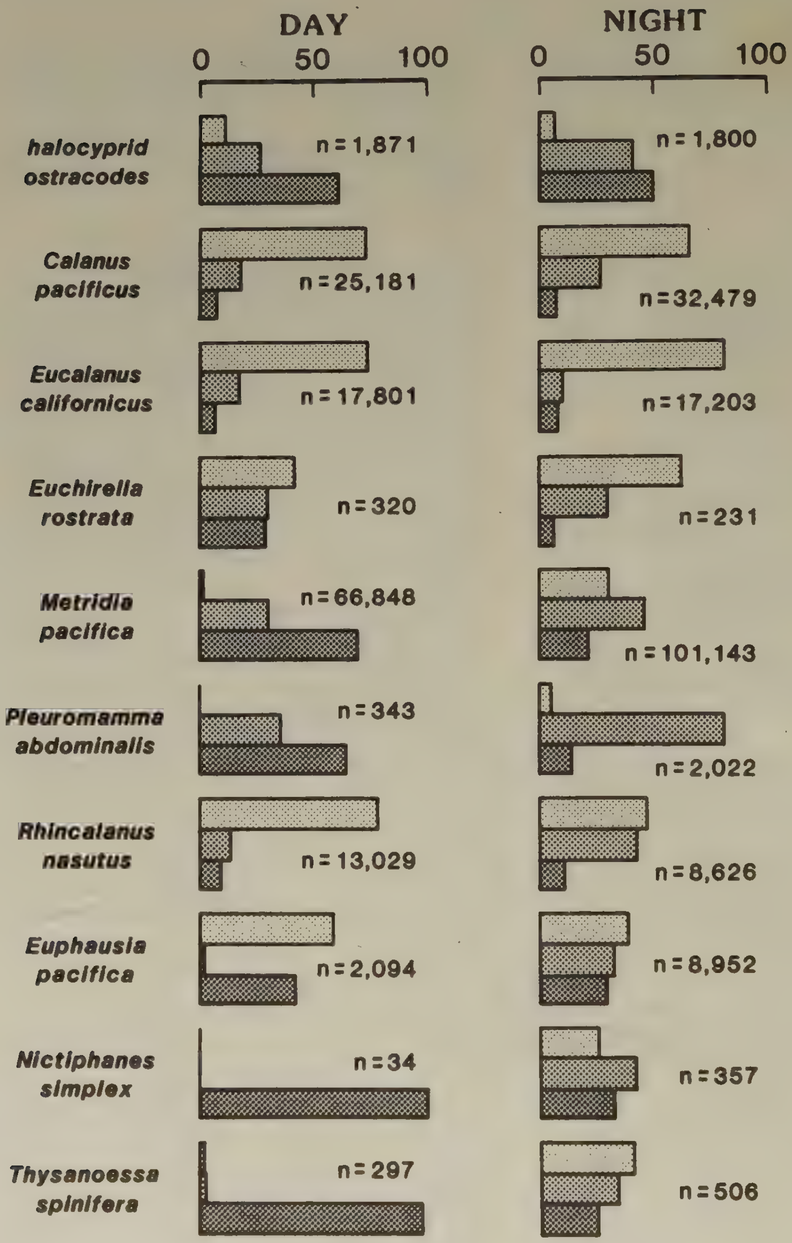

Figure 3. Diel vertical distribution patterns of the major prey taxa (those taxa occurring in ≥ 5% of the *S. jordani* that contained food). Values are the percentage of mean numbers of each taxon collected from each depth: upper (*light*), 18 m; mid (*medium*), 55 m; and lower (*dark*), 119 m. *n* = the sum of the mean numbers collected from each depth.

### *Distribution of Prey*

Most of the major prey taxa were more numerous at higher levels of the water column at night than during the day (Figure 3). (The many *E. pacifica* in the upper level by day, shown in Figure 3, resulted from a single large collection of 5–11-mm juveniles; those shown at the lower levels were 5–24-mm juveniles and adults.) Although net avoidance may have contributed to the discrepancy between day and night *n* values in Figure 3, we have no evidence of this. Most collections were taken at least 18 m above the bottom, but one plankton collection taken over the shelf during midday (15 min. at a depth of 218 m) inadvertently sampled close to the bottom (striking it at least once, as evidenced by a variety of strictly benthonic organisms in the catch). This collection, which included 46,720 *E. pacifica* (nearly four times the number we took in any other plankton collection) suggests that members of this species and perhaps others are more abundant close to the seafloor on the shelf during the day.

A series of collections at the Ascension Canyon site provided some detail on the nocturnal horizontal distribution of *E. pacifica* and other euphausiids over the shelf in relation to the canyon. During seven cruises between November 1980 and September 1982 we made 10 series of four successive oblique hauls, including 3 series that were replicated (all collections were taken between 2300 and 0330 h). Each haul was from a depth of 106 m to the surface and lasted 10 minutes; the first haul of each series sampled over the canyon; the next three sampled at 3.7-km intervals away from the northern rim of the canyon along the 137-m depth contour on the adjacent shelf.

The numerical proportion of *E. pacifica* collected above the canyon was significantly greater than that from any of the stations above the shelf. The mean proportions were: above canyon—46.77%; at 3.7 km—22.87%; at 7.4 km—18.02%; and at 11.1 km—18.68% (analysis of variance of arc sin transformations of percentages $F = 3.96$, $P = 0.02$, df 3,24; Newman-Keuls multiple comparison of means for gap order 2, difference = 19.95; for gap order 3, difference = 24.14; and for gap order 4, difference = 26.66). But although the proportions of *E. pacifica* collected from the shelf stations tended to be progressively less with distance from the canyon, the differences were not significant. In contrast, *Thysanoessa spinifera*, the euphausiid second in importance in the diet of *S. jordani*, was more evenly distributed over both the canyon and shelf, because there was no significant difference in its abundance among these collections ($F = 1.16$, df = 3,24).

Additional information on the distribution of prey species comes from comparing the diet of *S. jordani* between different areas. For example, the generally oceanic *E. pacifica* (Brinton 1962) dominated the diet of shortbellies taken near Ascension and Sur canyons, but the more neritic *T. spinifera* was more important to the diet of shortbellies taken off Pescadero Point and near Monterey Canyon (Table 5).

TABLE 5
**Mean Numbers of *Euphausia pacifica* and *Thysanoessa spinifera* in Gut Contents of *Sebastes jordani* from Different Areas**

| | Ascension Canyon ($n$ = 516) | Sur Canyon ($n$ = 18) | Pescadero Point ($n$ = 104) | Monterey Bay ($n$ = 56) |
|---|---|---|---|---|
| *E. pacifica* | 13.93 | 13.56 | 4.91 | 1.99 |
| *T. spinifera* | 0.78 | 0.05 | 14.13 | 3.47 |

## DISCUSSION

It is evident that *S. jordani* was distributed on the coastal shelf in relation to the distribution of its prey. This appeared true even though the normal habitat of its major prey, *Euphausia pacifica*, is beyond the shelf break at depths below 200 m (Brinton 1976). This could explain why shortbelly rockfish were concentrated along the shelf margin, especially adjacent to certain submarine canyons (Figure 1). Certain other shelf predators are known to feed heavily on deepwater organisms when these intermittently enter the shelf habitat. For example, *Sebastes pinniger* and *S. flavidus* off central Oregon feed primarily on *E. pacifica* above the outer shelf, with the former foraging mainly by day near the bottom (Brodeur and Pearcy 1984).

It is known that some oceanic organisms that perform diel vertical migrations are carried or disperse over the coastal shelf when in the surface waters at night. It has been suggested that when these organisms attempt to regain their normal daytime depths in the morning, many become trapped on the relatively shallow shelftop, where they are vulnerable to shelf-dwelling predators (Isaacs and Schwartzlose 1965; Pereyra et al. 1969; Clarke 1984). Apparently this mechanism is important in the trophic dynamics of *S. jordani*, because despite foraging at night on a variety of organisms in the water column, members of this species that were examined during this study had fed most intensively by day near the bottom—primarily on *E. pacifica* (Table 4). Clearly *E. pacifica* is especially vulnerable in this setting, probably because it is an open-water species that is maladapted to conditions close to or on the seafloor. On the other hand, *Thysanoessa spinifera* and *Nyctiphanes simplex*, which appear to be more neritic, did not share the diurnal vulnerability of *E. pacifica*. (*S. jordani* preyed most intensively on these two species in the water column at night; Table 4.) As shelf residents, they would be expected to possess adaptive defenses against threats characteristic of that habitat.

Probably *E. pacifica* is transported above the shelf at night by the coastal undercurrent. This current flows poleward above the shelf or upper continental slope throughout the year, but during most years reaches the surface only during fall and winter. At other times of year it is usually submerged, reportedly at depths of 200 to 500 m during the summer (Wyllie 1966; McLain and Thomas 1983). Chelton et al. (1987) found the undercurrent's velocities to be poleward at depths between 70 and 470 m throughout an 18-month period. So most of the time, at least, this current should be expected to impinge most directly on and flow over those parts of the shelf that extend offshore. This would account for the concentrations of *E. pacifica* at the Ascension and Sur canyon sites (Table 5). The dominance of *E. pacifica* near the northern rims of the canyons is consistent with this view. Because these locations are prominent projections in the path of the undercurrent (Figure 1), euphausiids ascending from the depths of adjacent canyons or downstream offshore areas would be expected to be carried over the shelf.

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## LITERATURE

Brinton, E. 1962. The distribution of Pacific euphausiids. *Bull. Scripps Inst. Oceanogr.* 8(2):51–270.

———. 1976. Population biology of *Euphausia pacifica* off southern California. *Fish. Bull., U.S.* 74:733–762.

Brodeur, R., and W. Pearcy. 1984. Food habits and dietary overlap of some shelf rockfishes (genus *Sebastes*) from the northeastern Pacific Ocean. *Fish. Bull., U.S.* 28:269–292.

Chelton, D. B., R. L. Bernstein, A. Bratkovich, and P. M. Kosro. 1987. The central California coastal circulation study. *EOS* 68(1): 1–6.

Clarke, T. A. 1984. Diet and morphological variation in snipefishes, presently recognized as *Macrorhamphosus Scolopax*, from southeast Australia: evidence for two sexually dimorphic species. *Copeia* 1984:595–608.

Gunderson, D. R., and T. M. Sample. 1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. *Mar. Fish. Rev.* 42(3):2–16.

Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull., U.S.* 72:915–1031.

Hobson, E. S., and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fish. Bull., U.S.* 74:567–598.

Hopkins, T. L., R. C. Baird, and D. M. Milliken. 1973. A messenger-operated closing trawl. *Limnol. Oceanogr.* 18:488–490.

Isaacs, J. D., and R. A. Schwartzlose. 1965. Migrant sound scatterers: interaction with the sea floor. *Science* (Wash., D.C.) 150:1810–1813.

Lenarz, W. H. 1980. Shortbelly rockfish, *Sebastes jordani*: a large unfished resource in waters off California. *Mar. Fish. Rev.* 42(3–4):34–40.

McLain, D. R., and D. H. Thomas. 1983. Year-to-year fluctuations of the California countercurrent and effects on marine organisms. *Calif. Coop. Oceanic Fish. Invest. Rep.* 24:165–181.

Merkel, T. J. 1957. Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. *Calif. Fish Game* 43:249–270.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. *Calif. Dep. Fish Game Fish Bull.* 157, 235 pp.

Pereyra, W. T., W. G. Pearcy, and F. E. Garvey, Jr. 1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. *J. Fish. Res. Board Can.* 26:2211–2215.

Phillips, J. B. 1964. Life history studies on ten species of rockfish (genus *Sebastodes*). *Calif. Dep. Fish Game Fish Bull.* 126, 70 pp.

Wyllie, J. G. 1966. Geostrophic flow of the California Current at the surface and at 200 meters. *Calif. Coop. Oceanic Fish. Invest. Atlas* no. 4, 288 pp.

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# A COPROLOGICAL SURVEY OF HELMINTH PARASITES OF THE HAWAIIAN MONK SEAL FROM THE NORTHWESTERN HAWAIIAN ISLANDS

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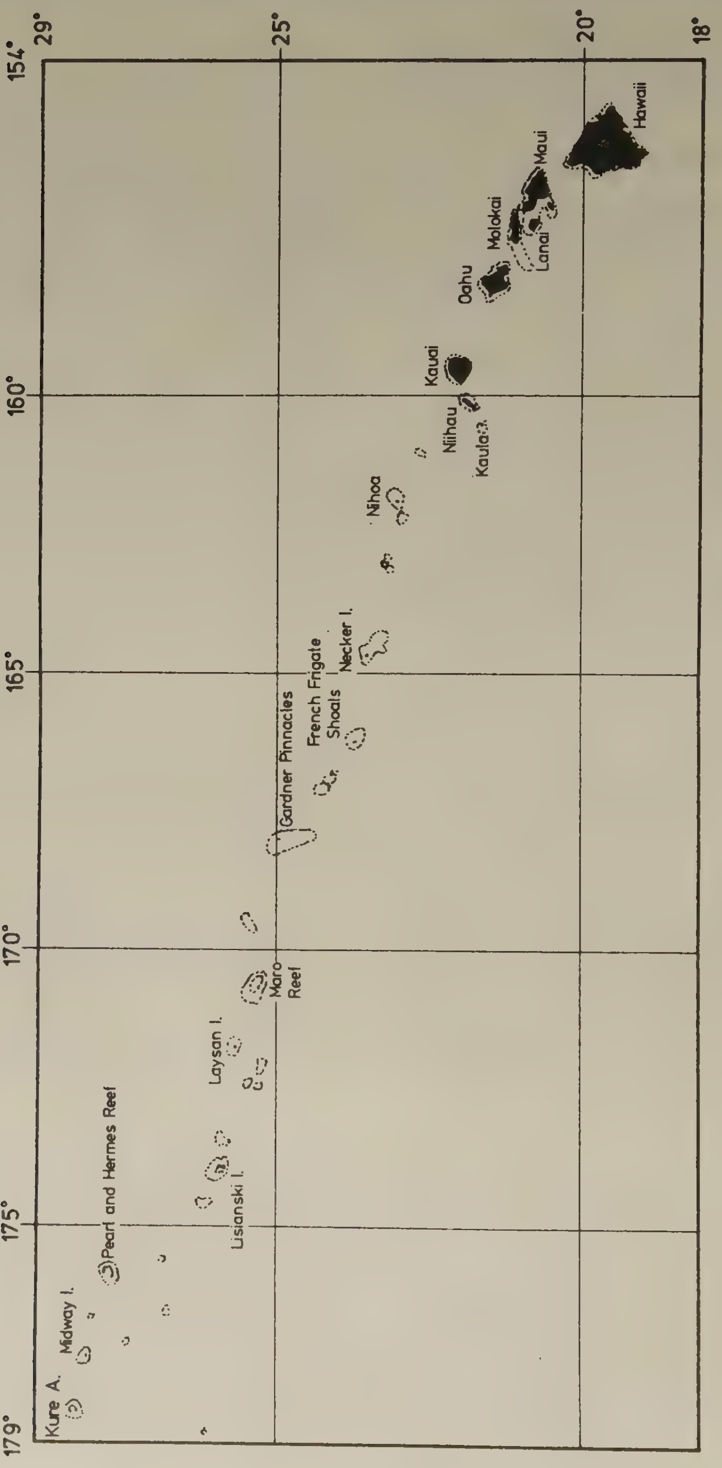
## Abstract

In conjunction with an Hawaiian monk seal, *Monachus schauinslandi*, breeding enhancement program, fecal samples were examined for the presence of helminth parasite products (eggs, larvae, and proglottids). Eighty-two samples were examined from four island groups in the northwestern Hawaiian Islands: 38 from Kure Atoll, 32 from French Frigate Shoals, 11 from Laysan Island, and one from Lisianski Island. Identified helminth products include those of *Diphyllobothrium* sp., *D. cameroni*, *Contracaecum turgidum*, *Anisakis* sp., *Corynosoma rauschi*, and Trematoda. In addition, eggs from *Halarachne laysanae* (Acari) were found in 3 samples. Eggs of *C. turgidum* were present in the highest percentage (>64%) of samples from all locations. Eggs of *Anisakis* sp. and Trematoda are reported from this host for the first time.

Key words: Hawaiian monk seal, *Monachus schauinslandi*, helminth parasites, coprological survey.

The genus *Monachus* includes three species: *M. monachus*, *M. schauinslandi*, and *M. tropicalis*, all considered endangered; of these, the Caribbean monk seal (*M. tropicalis*) is believed to be extinct (Kenyon 1977, Le Boeuf *et al.* 1986). For the past several decades the Hawaiian monk seal (*M. schauinslandi*) has declined sharply within its breeding range in the northwestern Hawaiian Islands (NWHI) (Kenyon and Rice 1959, Rice 1969, Johnson *et al.* 1982), from Nihoa Island northwesterly to Kure Atoll (Fig. 1). Recent studies on the inter-island movement of Hawaiian monk seals (Johnson and Kridler 1983, Stone 1984, Johanos and Kam 1986) suggest that although some movement occurs


154°
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179°
29°
25°
20°
18°
Hawaii
Maui
Molokai
Lanai
Oahu
Kauai
Niihau
Kaula
Nihoa
Necker I.
French Frigate Shoals
Gardner Pinnacles
Maro Reef
Laysan I.
Lisianski I.
Pearl and Hermes Reef
Midway I.
Kure A.

*Figure 1.* Map of the Hawaiian Archipelago showing sampling locations.

among the islands, in general the seals have a high fidelity to the beaches where they are born.

In 1984, the Marine Mammals and Endangered Species Program at the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory, began relocation of three to five young female monk seals per year from French Frigate Shoals to Kure Atoll to enhance reproduction. Concern that there may be some potential for spread of parasitic infections to the Kure Atoll population prompted this survey.

Although the Hawaiian monk seal has not been studied extensively, helminths reported include: four species of cestodes, *Diphyllobothrium hians* (Markowski 1952) = *Bothriocephalus* sp. (Chapin 1925), *D. elegans* and *D. cameroni* (Rausch 1969), and *D. rauschi* (Andersen 1987) = *D. hians* (Rausch 1969); one species of nematode, *Contracaecum turgidum* (Chapin 1925); one species of acanthocephalan, *Corynosoma rauschi* (Golvan 1959). In addition, one species of lung mite, *Halarachne laysanae* (Furman and Dailey 1980), has also been reported. This survey represents the first time trematode or *Anisakis* sp. (Nematoda) eggs have been reported from Hawaiian monk seals.

The terminology used herein follows that set forth by Margolis *et al.* (1982).

## MATERIALS AND METHODS

During the 1985 field season, fresh fecal samples (all under 24 h old) were collected from the beaches of four island groups (Kure, Laysan, Lisianski, and French Frigate Shoals) in the NWHI. Beaches were checked at least once daily for fresh scats. Many (30) samples were from individually identifiable seals, which were knowingly sampled only once, and represented all age and sex groups. The remaining scats were collected from unidentified seals, but of known size and sex, or collected from the beach without any information on the source seal. The latter group of samples were certain to be from individual seals because they were collected in areas of low seal density where it was easy to follow seal tracks on the sandy beach. The possibility exists that a few samples from the nonidentified seals may be duplicates from the same seal, collected days or weeks apart. The summary findings reported reflect the percentage of samples (not individuals) that were positive for a particular parasite.

All collected material was fixed in 70% ethanol or 10% formalin, and transported to the laboratory. After suspending the material in the fluid medium a drop of the suspension was placed on a slide, under a coverslip and examined under a light microscope. Magnifications of between 40 × and 400 × were used.

Whole mounts of cestodes and acanthocephalans from necropsied seals and cestode proglottids from scat samples were placed in 70% ethanol. They were then stained with Semichon's carmine, destained in 1% acid alcohol, dehydrated in an ethanol series, cleared in xylene, and mounted on slides, under coverslip in Permount.

Whole nematodes from necropsied seals were cleared in glycerine alcohol and mounted on slides, under coverslip in glycerine jelly.

*Table 1.* Numbers and percents of fecal samples from monk seals infected with different parasites; percents are in parentheses.

| No. of parasites | Number and percent of samples | | | |
|---|---|---|---|---|
| | Kure $n = 38$ | French Frigate Shoals $n = 32$ | Laysan Island $n = 11$ | Lisianski Island $n = 1$ |
| No parasites | 0 | 1 (3.1) | 0 | 0 |
| One parasite | 5 (13.2) | 9 (28.1) | 2 (18.2) | 0 |
| Two parasites | 12 (31.6) | 15 (46.9) | 2 (18.2) | 0 |
| Three parasites | 17 (44.7) | 6 (18.8) | 7 (63.6) | 0 |
| Four parasites | 4 (10.5) | 1 (3.1) | 0 | 1 (100) |

## RESULTS

Analysis of the samples indicated that parasitism was highly prevalent in the seals from all sites sampled. Of the 82 samples examined, 81 (98.8%) were positive for parasite products of some type (eggs, larvae, or proglottids): all samples from Kure Atoll, Laysan Island, and Lisianski Island and 31 of 32 (97%) from French Frigate Shoals (Table 1). The numbers and percentages of fecal samples infected with different parasites are in Table 1. The prevalence of parasite products in fecal samples from each location and the probable identity of those parasites are in Table 2.

*Cestoda—Diphyllobothrium* sp. eggs were found in fecal samples from all locations: Kure Atoll 26 of 38 (68.4%), French Frigate Shoals 9 of 32 (28.1%), Laysan Island 3 of 11 (27.3%), and Lisianski Island 1 of 1 (100%). These eggs were identified as such on the basis of their size (average 0.047 mm × 0.035 mm) and shape, and by cross matching them with eggs teased from the mature proglottids of *D. cameroni* collected from two necropsied Hawaiian monk seals, one each from Kure Atoll and Laysan Island. These *Diphyllobothrium* sp. could not be identified to species because congeners have similar eggs. Gravid proglottids were found in 3 samples, 2 from Kure Island and 1 from French Frigate Shoals. The proglottids were identified as *D. cameroni* on the basis of shape (length/width ratio, approximately 1:3), possessing a single genital opening located midventrally at the anterior end of the segment, and covered by velum of the preceding segment, and possessing eggs of the same size (*see* above) and ellipsoidal shape.

*Nematoda*—Eggs of *Contracaecum turgidum* were the most prevalent parasite product identified (>63% at all locations). These eggs were identified as such by their spherical shape and size (0.054–0.060 mm, average 0.056 mm). Samples were cross matched with eggs from whole *C. turgidum* collected from necropsied seals on French Frigate Shoals (2), Kure Atoll (1), and Laysan Island (1).

Eggs of *Anisakis* sp. were found in samples from all locations at >53% prevalence. These eggs were identified as such on the basis of their characteristic

*Table 2.* Numbers and percents of fecal samples containing different types of parasite products at each location; percents are in parentheses.

| | Number and percent of parasite products | | | |
|---|---|---|---|---|
| Parasite | Kure Atoll *n* = 38 | French Frigate Shoals *n* = 32 | Laysan Island *n* = 11 | Lisianski Island *n* = 1 |
| *Diphyllobothrium* sp. | 26 (68.4) | 9 (28.1) | 3 (27.3) | 1 |
| *Contracaecum turgidum* | 33 (86.8) | 28 (87.5) | 7 (63.6) | 1 |
| *Anisakis* sp. | 28 (73.7) | 17 (53.1) | 7 (63.6) | 1 |
| Trematoda | 4 (10.5) | 3 (9.4) | 1 (9.1) | 1 |
| *Corynosoma rauschi* | 4 (10.5) | 2 (6.3) | 0 | 0 |
| *Halarachne laysanae* | 1 (2.6) | 2 (6.3) | 0 | 0 |

features (embryonic material not filling entire shell) as given by Dailey and Gilmartin 1980. This represents the first report of this genus from Hawaiian monk seals.

*Trematoda*—A low prevalence of trematode eggs was found at Kure Atoll (4 of 38; 10.5%), French Frigate Shoals (3 of 32, 9.4%), and Laysan Island (1 of 11, 9.1%). The eggs were identified as Trematoda on the basis of a pronounced operculum and ovoid shape. Trematodes have not been previously reported from this host and cross matching from whole specimens was not possible. Therefore, this identification has not been verified and should be regarded as a probable finding.

*Acanthocephala*—Eggs of *Corynosoma rauschi* were found in samples from Kure Atoll (4 of 38, 10.5%) and French Frigate Shoals (2 of 32, 6.3%) whereas samples from Laysan and Lisianski Islands were negative. These eggs were cross-matched with eggs from four whole specimens from one necropsied seal at French Frigate Shoals. The type location for this parasite, as reported by Golvan (1959), is Midway Island.

*Acari*—Eggs of *Halarachne laysanae* were found in samples from Kure Atoll (1 of 38, 2.6%) and French Frigate Shoals (2 of 32, 6.3%). Samples from Lisianski and Laysan Islands were negative although the latter is the type location for the parasite (Furman and Dailey 1980).

## Discussion

The data show that no new parasitic infections will be introduced to a previously uncontaminated area when moving animals from French Frigate Shoals to Kure Atoll. Given that Kure Atoll and French Frigate Shoals are at opposite ends of the NWHI and the fact that there is some inter-island movement occurring among the Hawaiian monk seals, the authors would expect to see a continuum of these parasite infections throughout the NWHI. The lack of a continuum shown here from Laysan and Lisianski Islands can most likely be attributed to small sample sizes: While rates of infection vary, the population as a whole is apparently homogeneous in terms of types of parasite infections present.

No statistics are available on the percentages of parasite-caused mortality in the Hawaiian monk seal. However, infection by *Contracaecum* sp. and resulting gastrointestinal ulcers have been implicated in the death of a Hawaiian monk seal (Whittow *et al.* 1979). Infections by ascaridoid nematodes, to which *Contracaecum* sp. and *Anisakis* sp. belong, is considered to be a significant mortality factor in other pinniped populations (Keyes 1965).

Deardorff *et al.* (1982) examined 134 species of finfishes (29 families) and 8 species of invertebrates (7 families) from the main Hawaiian Islands. All specimens examined were found to be infected with at least one of eight species of ascaridoid larvae: two species of *Anisakis,* three of *Hysterothylacium,* one of *Raphidascaris,* and one of *Terranova.* A summary of food items from Hawaiian monk seal scat and regurgitation samples (Gilmartin, personal observation) shows that many of the prey species are of the same families as those reported by Deardorff *et al.* (1982) as infected with ascaridoid worms. While the distance between the southeast and northwest Hawaiian Islands is hundreds of miles, infected individuals of the same families may serve as the intermediate host for some of the parasite infections in the Hawaiian monk seal.

## LITERATURE CITED

ANDERSEN, K. I. 1987. A redescription of *Diphyllobothrium stemmacephalum* Cobbold, 1858 with comments on other marine species of *Diphyllobothrium* Cobbold, 1858. Journal of Natural History 21:411–427.

CHAPIN, E. A. 1925. Descriptions of new internal parasites. Proceedings U.S. National Museum 68 (Art 2):1–4.

DAILEY, M. D., AND W. G. GILMARTIN. 1980. Diagnostic key to the parasites of some marine mammals. Naval Ocean Systems Center, San Diego, CA Technical Document #295. 37 pp.

DEARDORFF, T. L., M. M. KLIKS, M. E. ROSENFELD, R. A. RYCHLINSKI AND R. S. DESOWITZ. 1982. Larval ascaridoid nematodes from the fishes near the Hawaiian Islands, with comments on the pathogenicity experiments. Pacific Science 36:187–201.

FURMAN, D. P., AND M. D. DAILEY. 1980. The genus *Halarachne* (Acari: Halarachnidae), with the description of a new species from the Hawaiian monk seal. Journal of Medical Entomology 17:352–359.

GOLVAN, Y. J. 1959. Acanthocephales du genre *Corynosoma* Luhe 1904. Parasites de mammiteres d'Alaska et de Midway. Annales Parasitologie Humaine et Compareé 34:288–321.

JOHANOS, T. C., AND A. K. H. KAM. 1986. The Hawaiian monk seal on Lisianki Island 1983. U.S. Dept. of Commerce, NOAA, Technical Memo, NMFS, NOAA-TM-NMFS-SWFC-47. 33 pp.

JOHNSON, A. M., R. L. DELONG, C. H. FISCUS AND K. W. KENYON. 1982. Population status of the Hawaiian monk seal (*Monachus schauinslandi*) 1978. Journal of Mammalogy 63:415–421.

JOHNSON, A. M., AND E. KRIDLER. 1983. Inter-island movement of Hawaiian monk seals. (Elepaio) Journal of the Hawaiian Audubon Society 44:43–45.

KENYON, K. W. 1977. Caribbean monk seal extinct. Journal of Mammalogy 53: 97–98.

KENYON, K. W., AND D. W. RICE. 1959. Life history of the Hawaiian monk seal. Pacific Science 13:215–252.

KEYES, M. D. 1965. Pathology of the northern fur seal. Journal of the American Veterinary Medical Association 147:1090–1095.

LE BOEUF, B. J., K. W. KENYON AND B. VILLA-RAMIREZ. 1986. The Caribbean monk seal is extinct. Marine Mammal Science 2:70–72.

MARGOLIS, L., G. W. ESCH, J. C. HOLMES, A. M. KURIS AND G. A. SCHAD. 1982. The use of ecological terms in parasitology (Report of an adhoc committee of the American Society of Parasitologists). Journal of Parasitology 68:131–133.

MARKOWSKI, S. 1952. The cestodes of pinnipeds in the Arctic and other regions. Journal of Helminthology 26:171–214.

RAUSCH, R. L. 1969. Diphyllobothriid cestodes from the Hawaiian Monk Seal, *Monachus schauinslandi* Matschie, from Midway Atoll. Journal of the Fisheries Research Board of Canada 26:947–956.

RICE, D. W. 1969. Population dynamics of the Hawaiian monk seal. Journal of Mammalogy 41:376–385.

STONE, H. S. 1984. Hawaiian monk seal populations research, Lisianski Island 1982. U.S. Dept. of Commerce, NOAA, Technical Memo, NMFS, NOAA-TM-NMFS-SWFC-47. 33 pp.

WHITTOW, G. C., G. H. BALAZS AND G. D. SCHMIDT. 1979. Parasitic ulceration of the stomach in the Hawaiian Monk Seal *Monachus schauinslandi*. (Élepaio) Journal of the Hawaiian Audubon Society 38:83–84.

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# SURVIVORSHIP PATTERNS IN THREE SPECIES OF CAPTIVE CETACEANS

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## Abstract

Survival rates for three species of captive cetaceans are reported, based on records of dates of capture, birth, and death of individual animals. The annual survival rate was 0.93 for bottlenose dolphins and killer whales and 0.94 for white whales. Confidence limits of these estimates are discussed. Differences in survival rates between institutions were significant for bottlenose dolphins only. Calf survival for bottlenose dolphins was lower than non-calf survival. Survivorship of male killer whales was significantly less than survivorship of female killer whales; sex-specific survival rates were similar for the other two species. Estimates of average or maximum longevity alone were not useful in comparing rates of survival. Because survival in the first year of captivity may be lower than subsequent years, estimates of the expected lifespan, based on data from the first few years of captivity, may be biased.

Key words: survival, captivity, cetaceans, *Tursiops, Orcinus, Delphinapterus.*

Many species of marine mammals, especially cetaceans and pinnipeds, are maintained in captivity for purposes of public display and scientific research. In 1983 over 1,300 marine mammals, including more than 300 bottlenose dolphins (*Tursiops truncatus*), were held in oceanaria and zoological parks around the world (Duffield and Dimeo-Ediger 1984). The U.S. Marine Mammal Protection Act of 1972 (MMPA) and similar legislation in other countries recognize that marine mammals are resources of great aesthetic and recreational, as well as economic, significance. Over the last 15 yr, some individuals and groups have questioned the ethics of capturing and maintaining marine mammals in captivity for purposes of either public display or scientific research, particularly dolphins and larger cetaceans (*see* the Proceedings from the "Whales Alive" Conference, 1983; Journal of Mammalogy 65:740–741). One reason for this is the concern that the apparent longevity of captive animals is substantially less than that of their counterparts in the wild. Another reason is differences in the ability of different institutions to care for and maintain marine mammals, particularly cetaceans, in captivity.

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The primary objectives of this study were to: (1) estimate the post-capture survival rates for three species of cetaceans (bottlenose dolphins; white whales, *Delphinapterus leucas*; and killer whales, *Orcinus orca*) commonly held in captivity for purposes of scientific research and public display, and (2) determine whether survival rates vary significantly by institution, age, or sex. Secondary objectives were to determine, if possible, whether survival in captivity differs significantly from survival in the wild, and to provide estimates of the expected longevity of each of the three species in captivity.

## METHODS

The data used in this analysis were obtained from the inventory of captive marine mammals maintained by the National Marine Fisheries Service (referred to as the Marine Mammal Inventory Report). These data are provided to the Service as part of the requirements for obtaining a permit to capture and maintain marine mammals for public display. The Marine Mammal Inventory Report, therefore, does not include all marine mammals held in captivity, but does represent a significant portion of marine mammals held in captivity in the U. S. and elsewhere. The following information for 864 bottlenose dolphins, 40 killer whales, and 48 white whales was transcribed into a data base: institution, animal identification number, number of days survived in captivity, whether or not the animal was alive at the end of the reporting period, sex, age (calf or non-calf), and date of acquisition. For a few animals the date of acquisition was not provided in the inventory; these animals were not included in the analysis. Finally, stillbirths were not included in the analysis. The number of days survived in captivity was calculated using a technique presented by Poole *et al.* (1981) and was based on the date of acquisition and either the date of the Inventory Report, the date of death, or the date the animal was transferred to a different institution.

The method for estimating rates of survival was taken from Trent and Rongstad (1974). This technique is similar to the estimator used by Mayfield (1975), except that information on an animal's survival is available on a daily basis. With this approach, animal-days are based on the number of days that an individual could have successfully survived. Obviously, once an animal has died, additional animal-days for that individual can not be accumulated. Recent work by Bart and Robson (1982) and Heisey and Fuller (1985) suggest that because the sampling interval is fixed at one day, the simple estimator suggested by Trent and Rongstad is a maximum likelihood estimate.

The following methodology was used to calculate annual survival rates:

$$\mathrm{DSR} = 1 - \sum_{i=1}^{K} (y_i) / \sum_{i=1}^{K} (x_i) \tag{1}$$

where DSR is the daily survival rate, $Y_i$ is one if the $i$th individual died during the reporting period and zero if the $i$th individual survived through the entire reporting period, $x_i$ is the total number of days, including any days in which deaths may have occurred, in the reporting period for the $i$th individual, and $K$ is the number of animals in the sample. The summation of $y$ over all animals is the total number of deaths that occurred; the summation of $x$ over all animals is the total number of animal-days observed. The daily survival rate was converted to an annual survival rate (ASR) by raising the DSR to the 365.25th power (*i.e.*, the average number of days in a year).

There are two assumptions that must be met in using this method (Trent and Rongstad 1974): (1) the death of one individual does not affect the probability of another individual surviving (*i.e.*, animal-days are independent sample periods), and (2) there is a constant probability of surviving each day. If these two assumptions are met and because each animal-day can have only one of two outcomes, survival or death, each individual animal-day is a binomial event. Therefore, the probability an animal survives $x$ days is simply the daily survival rate raised to the power of $x$ and the distribution of deaths over that period will be distributed binomially.

Both assumptions seem reasonable. With regard to the first, dates of death appear to be independent for animals at any institution for any of the three species. That is, there were no apparent concentrations of mortalities by date for any institution. With regard to the second assumption, it is conceivable that husbandry practices have improved significantly over the last 20 yr and are continuing to improve. Klinowska and Brown (unpublished manuscript prepared for the Department of the Environment, United Kingdom 1986) reported that husbandry practices in the United Kingdom, as indicated by an analysis of mortality rates for some cetacean species, have improved, at least since 1980. However, in the analysis of these data we found no difference between the mean survival rate for killer whales and white whales between 1975–1979 and 1980–1984. For bottlenose dolphins, however, where the sample size was considerably larger than for the other two species, the survival of animals in captivity between 1975 and 1979 was significantly less than the survival of animals between 1980 and 1984. However, because most of the available data are from animals held in captivity since 1980, there was no difference between the pooled survival rate for all years and the survival rate based on data from animals held in captivity between 1980 and 1984.

Another source of bias in estimating the average survival of animals held in captivity would occur if survival were not constant with age. It was not possible to test for age effects on survival of captive killer whales and white whales because of a lack of either known-age or captive born animals. For bottlenose dolphins, it was possible to compare the survival rates of young of the year and one year old animals. The survival of one year old bottlenose dolphins was not significantly different from the survival rate of non-calves (*see* Results). Because of the small number of known-age animals that were older than 10 yr of age, it was not possible to test for differences in the survival rate of animals as they approach the age of maximum longevity.

A 95% confidence interval for the DSR was calculated directly from a binomial distribution, where the binomial parameter was set equal to (1-DSR) and *n* was set equal to the total number of animal-days. The upper and lower limits (probabilities of 0.025 and 0.975, respectively) for the number of deaths were interpolated to the nearest 0.01 animal. These limits, after being divided by *n* and subtracted from 1.0, were raised to the 365.25 power to determine the confidence interval for the ASR.

For example, if six mortalities were observed over 10,000 animal-days, the DSR would be 0.9994 (1 − 0.0006) and the ASR would be 0.80 (0.9994 raised to the 365.25 power). Using the standard formula for the frequency distribution of a binomial distribution (Freund 1971), one can calculate that the probability of having one or zero deaths in a given year is 0.02; the probability of having two or fewer deaths in a given year is 0.06. Therefore, the lower limit (*i.e.*, $P = 0.025$) for the number of deaths was estimated to be 1.17 by linear interpolation. Likewise, the upper limit to the number of deaths was estimated to equal 10.77. The 95% confidence interval for the ASR is then calculated as:

$$\text{upper limit} = (1 - 1.17/10{,}000)^{365.25} = 0.96$$

$$\text{lower limit} = (1 - 10.77/10{,}000)^{365.25} = 0.67$$

For most of the calculations, the lower and upper limits for the expected number of deaths was calculated directly from the binomial distribution, given a certain number of deaths and animal-days. However because of machine limitations in handling large factorials, we used a normal approximation to estimate the upper limit for the number of deaths when the observed number of deaths was greater than five. In this approximation, we assumed that the mean number of deaths equals the observed number of deaths and that the standard deviation of the number of deaths for a particular institution equals the square root of the mean number of deaths. The upper limit for the mean number of deaths was estimated as the product of 1.96 and the standard deviation of the number of deaths plus the mean number of deaths. Differences between survival rates were tested using the variance test for homogeneity of the binomial distribution (Snedecor and Cochran 1967). A 95% confidence interval around the median survival rate was calculated in the usual fashion (Snedecor and Cochran 1967).

## RESULTS

### *Bottlenose Dolphins*

The mean annual survival rate of 864 bottlenose dolphins was 0.93; the 95% confidence interval was 0.92–0.94 (Table 1). The median rate of survival for the 57 institutions listed in Table 1 was 0.94. The 95% confidence interval around the median was slightly greater than the 95% confidence interval around the mean. The distribution of survival rates by institution was skewed towards higher values with a modal value of 1.00.

Significant differences were found among survival rates for the 57 institutions listed in Table 1 ($P < 0.005$). Because the statistical test employed is based on the expected number of mortalities per animal-day per institution and because institutions with less than 20,000 animal-days would have fewer than five expected mortalities, we reanalyzed the data using data from only those institutions where the expected number of mortalities was greater than four. Again we found significant differences in the survival rate among institutions ($P < 0.025$). To identify those institutions that had a significantly different survival rate from the overall mean survival rate, we compared the survival rate of each institution with the pooled survival rate of all other institutions. Six institutions were found to have survival rates that were significantly below the average rate of survival for all 57 institutions; two institutions had survival rates that were significantly better than the average survival rate of all institutions (Table 1).

The minimum ASR for the 57 institutions listed in Table 1 was 0.01. The institution responsible for this extremely low survival rate (Table 1: #34) had accumulated only 168 dolphin-days. The minimum ASR for institutions that had at least 3,650 dolphin-days experience (*i.e.,* ten dolphin-years) was 0.75 (Table 1: #47). The median ASR for the 43 institutions with over 3,650 dolphin-days of experience was 0.94 (±0.02). There was no difference between the survival rate of male and female bottlenose dolphins (Table 2).

The survival rate of calves that were born in captivity was found to be significantly less than the survival rate of non-calves (Table 2). The annual survival rate of newborn animals was 0.61. The ASR of these animals increased to 0.97 after the first year (Table 3). This was not significantly different than the ASR of animals removed from the wild and maintained in captivity, but suggests that captive born animals that survive their first year may be better adapted to captive maintenance than animals removed from the wild. Obviously, more information is needed before a definitive statement can be made. The survival rate of non-calves that survived the first year of captivity was 0.95; this is not significantly different from the overall mean rate of survival (Table 3).

To test whether the differences between the survival rate of dolphins at a particular institution and the overall mean rate of survival was influenced by the age distribution of animals, we reanalyzed the data excluding information from animals less than one year old. All of the institution-specific survival rates that were reported in Table 1 to be significantly less than the mean rate of survival were still significantly less than the overall mean. With information excluded from animals less than one year old, only one institution had an average survival rate that was greater than the mean survival rate for all institutions.

Recently captured animals are infrequently acclimated to captivity at the institution that will permanently maintain them. Acclimation is generally assumed to occur between 30 and 90 d. To test whether the differences reported in Table 1 were related to institutional differences in the acclimation process, we compared the survival rate of non-calves that were known to have survived the first 90 d of captivity with the overall mean survival rate of non-calves. Four of the six institutions that had lower survival rates than the average were still found to have significantly lower survival rates than the average. Only one institution had an average survival rate that was greater than the average survival

*Table 1.* Summary of survival data for captive bottlenose dolphins. Data are from the National Marine Fisheries Service's Marine Mammal Inventory Reports. Data are through 10-11-85.

| # | # Animals | Live dolphin days | Deaths | Total | Average survival + (95% CI) |
|---|---|---|---|---|---|
| 1 | 1 | 341 | 0 | 341 | 1.00 (–) |
| 2 | 7 | 4,177 | 0 | 4,177 | 1.00 (–) |
| 3 | 16 | 6,001 | 2 | 6,003 | 0.89 (0.75–1.00) |
| 4 | 17 | 43,817 | 6 | 43,823 | 0.95 (0.91–0.99) |
| 5 | 1 | 657 | 0 | 657 | 1.00 (–) |
| 6 | 67 | 130,984 | 30 | 131,014 | 0.92 (0.89–0.95) |
| 7 | 9 | 31,809 | 4 | 31,813 | 0.96 (0.91–1.00) |
| 8 | 8 | 7,930 | 2 | 7,932 | 0.91 (0.79–1.00) |
| 9 | 2 | 2,137 | 2 | 2,139 | *0.71 (0.44–1.00) |
| 10 | 4 | 17,525 | 1 | 17,526 | 0.98 (0.94–1.00) |
| 11 | 10 | 18,341 | 4 | 18,345 | 0.92 (0.85–0.98) |
| 12 | 5 | 17,173 | 3 | 17,176 | 0.94 (0.88–1.00) |
| 13 | 3 | 1,645 | 0 | 1,645 | 1.00 (–) |
| 14 | 5 | 15,211 | 3 | 15,214 | 0.93 (0.87–1.00) |
| 15 | 3 | 5,376 | 1 | 5,377 | 0.93 (0.82–1.00) |
| 16 | 5 | 11,780 | 1 | 11,781 | 0.97 (0.91–1.00) |
| 17 | 5 | 11,508 | 4 | 11,512 | 0.88 (0.78–1.00) |
| 18 | 33 | 55,928 | 20 | 55,948 | *0.88 (0.83–0.93) |
| 19 | 2 | 10,850 | 0 | 10,850 | 1.00 (–) |
| 20 | 10 | 18,222 | 6 | 18,228 | 0.89 (0.81–0.98) |
| 21 | 8 | 10,000 | 3 | 10,003 | 0.90 (0.79–1.00) |
| 22 | 12 | 32,162 | 6 | 32,168 | 0.93 (0.88–0.99) |
| 23 | 23 | 75,597 | 9 | 75,606 | 0.96 (0.93–0.99) |
| 24 | 4 | 8,386 | 0 | 8,386 | 1.00 (–) |
| 25 | 7 | 22,735 | 2 | 22,737 | 0.97 (0.92–1.00) |
| 26 | 11 | 10,959 | 0 | 10,959 | 1.00 (–) |
| 27 | 7 | 13,887 | 3 | 13,890 | 0.92 (0.85–1.00) |
| 28 | 17 | 58,642 | 4 | 58,646 | *0.98 (0.75–1.00) |
| 29 | 8 | 15,204 | 0 | 15,204 | 1.00 (–) |
| 30 | 2 | 6,118 | 0 | 6,118 | 1.00 (–) |
| 31 | 6 | 11,527 | 1 | 11,528 | 0.97 (0.91–1.00) |
| 32 | 3 | 3,428 | 0 | 3,428 | 1.00 (–) |
| 33 | 2 | 2,470 | 1 | 2,471 | 0.86 (0.64–1.00) |
| 34 | 2 | 166 | 2 | 168 | *0.01 (0.00–1.00) |
| 35 | 11 | 8,119 | 4 | 8,123 | 0.84 (0.70–1.00) |
| 36 | 10 | 18,476 | 3 | 18,479 | 0.94 (0.87–1.00) |
| 37 | 6 | 1,341 | 0 | 1,341 | 1.00 (–) |
| 38 | 4 | 1,979 | 1 | 1,980 | 0.83 (0.57–1.00) |
| 39 | 155 | 214,765 | 72 | 214,837 | *0.88 (0.86–0.91) |
| 40 | 16 | 17,025 | 2 | 17,027 | 0.96 (0.90–1.00) |
| 41 | 2 | 590 | 1 | 591 | *0.54 (0.06–1.00) |
| 42 | 33 | 30,033 | 9 | 30,042 | 0.90 (0.83–0.96) |
| 43 | 4 | 2,116 | 1 | 2,117 | 0.84 (0.60–1.00) |
| 44 | 2 | 8,293 | 0 | 8,293 | 1.00 (–) |
| 45 | 6 | 1,965 | 1 | 1,966 | 0.83 (0.58–1.00) |
| 46 | 3 | 466 | 0 | 466 | 1.00 (–) |
| 47 | 5 | 3,753 | 3 | 3,756 | *0.75 (0.54–1.00) |
| 48 | 43 | 118,025 | 25 | 118,050 | 0.93 (0.90–0.95) |

*Table 1.* Continued.

| # | # Animals | Live dolphin days | Deaths | Total | Average survival + (95% CI) |
|---|---|---|---|---|---|
| 49 | 4 | 2,380 | 0 | 2,380 | 1.00 (–) |
| 50 | 16 | 23,493 | 8 | 23,501 | 0.88 (0.80–0.97) |
| 51 | 32 | 112,070 | 15 | 112,085 | 0.95 (0.93–0.98) |
| 52 | 10 | 14,172 | 1 | 14,173 | 0.97 (0.93–1.00) |
| 53 | 121 | 235,891 | 31 | 235,922 | *0.95 (0.94–0.97) |
| 54 | 17 | 33,101 | 7 | 33,108 | 0.93 (0.87–0.98) |
| 55 | 22 | 46,783 | 10 | 46,793 | 0.92 (0.88–0.97) |
| 56 | 7 | 30,332 | 2 | 30,334 | 0.98 (0.94–1.00) |
| 57 | 10 | 10,721 | 3 | 10,724 | 0.90 (0.80–1.00) |
| Totals | 864 | 1,618,582 | 319 | 1,618,901 | 0.93 (0.92–0.94) |

* An asterisk denotes that the institution-specific survival rate is significantly different from the survival rate pooled over all institutions.

rate of all institutions. The annual survival rate of non-calves, based on data from the first 90 d of captivity, was 0.53; significantly different from the industry-average of 0.93. Therefore, while this factor is generally not adequate in discriminating among institutions with poor, average, or good rates of survival, it does explain some of the differences between institution-specific rates of survival.

The institutional differences in the survival rate of dolphins reported in Table 1 does not seem to be related to the age composition (although only calf and non-calf survival were compared) or sex composition of the captive population. Also, it is only partially related to mortalities that occurred during the acclimation period. It is clear that institutions that rear a large number of calves, everything else being equal, will have an overall mortality rate that is greater than institutions that do not breed their animals in captivity. This effect may be partially offset by the slightly increased survival of non-calves that were born in captivity relative to captive animals that were not born in captivity.

It is also clear that the power of the test statistic is related to the total number of dolphin-days in the sample. Because of this, we recommend that investigators that apply this test statistic to a particular data set also provide the power of a particular test when the test results are insignificant. In our analysis, we would have been able to detect a significant difference between the survival rates of an

*Table 2.* Summary of average survival rate for bottlenose dolphins by sex and age (calf vs. non-calf). Data are from NMFS Marine Mammal Inventory Report, 1985.

| | | Days alive | Deaths | Average survival |
|---|---|---|---|---|
| Sex: | Male | 657,197 | 120 | 0.94 |
| | Female | 934,993 | 170 | 0.94 |
| Age: | Calf | 23,586 | 32 | 0.61 |
| | Non-calf | 1,495,340 | 276 | 0.93 |

*Table 3.* Summary of bottlenose dolphin survivorship, conditional on animal surviving the first year.

| Treatment | Days alive | Deaths | Average survivorship |
|---|---|---|---|
| All animals | 1,599,285 | 214 | 0.95 |
| Non-calves | 1,479,554 | 204 | 0.95 |
| Born in captivity | 119,731 | 10 | 0.97 |

institution and the pooled survival rate from all of the institutions reported in Table 1 if there would have been a difference of seven percentage points and a sample size of at least 20,000 dolphin-days from the institution that was being tested.

### *Killer Whales and White Whales*

The annual survival rate of 40 captive killer whales was 0.93 (Table 4); the 95% confidence interval was 0.90–0.96. The range of ASRs for the 10 institutions listed in Table 4 was 0.73 to 1.00. There were no significant differences in the ASR among the different institutions. Given the sample size reported in Table 4, institutional specific survival rates would have to be less than 0.86 with a sample size of 10,000 animal-days to be significantly different from the overall mean. With a sample size of 1,000 animal-days, the observed survival rate would have to be less than 0.69 to be significantly different from the overall mean.

The annual survival rate of 48 white whales was 0.94 ± 0.03 (Table 5). The range of ASRs for 9 institutions was 0.80 to 1.00. There were no significant differences in survival rates among the institutions. The power of this test was

*Table 4.* Summary of survival data for captive killer whales. Data are from National Marine Fisheries Service's Marine Mammal Inventory Report.

| # | Number animals | Live dolphin days | Deaths | Total | Average survival | 95% conf. int. |
|---|---|---|---|---|---|---|
| 1 | 1 | 656 | 0 | 656 | 1.00 | (–) |
| 2 | 5 | 15,110 | 2 | 15,112 | 0.95 | (0.89–1.00) |
| 3 | 4 | 6,907 | 1 | 6,908 | 0.95 | (0.85–1.00) |
| 4 | 2 | 3,344 | 1 | 3,345 | 0.90 | (0.72–1.00) |
| 5 | 18 | 39,943 | 9 | 39,952 | 0.92 | (0.87–0.97) |
| 6 | 3 | 2,859 | 1 | 2,860 | 0.88 | (0.68–1.00) |
| 7 | 2 | 3,437 | 1 | 3,438 | 0.90 | (0.73–1.00) |
| 8 | 2 | 20,264 | 1 | 10,265 | 0.97 | (0.90–1.00) |
| 9 | 1 | 2,486 | 0 | 2,486 | 1.00 | (–) |
| 10 | 2 | 2,276 | 2 | 2,278 | 0.73 | (0.45–1.00) |
| Totals | 40 | 87,282 | 18 | 87,300 | 0.93 | (0.90–0.96) |

*Table 5.* Summary of survival data for captive white whales. Data are from National Marine Fisheries Service's Marine Mammal Inventory Report.

| # | Number animals | Live dolphin days | Deaths | Total | Average survival | 95% conf. int. |
|---|---|---|---|---|---|---|
| 1 | 8 | 6,665 | 4 | 6,669 | 0.80 | (0.65–1.00) |
| 2 | 10 | 23,781 | 4 | 23,785 | 0.94 | (0.88–1.00) |
| 3 | 2 | 6,047 | 0 | 6,047 | 1.00 | (–) |
| 4 | 3 | 15,148 | 1 | 15,149 | 0.98 | (0.93–1.00) |
| 5 | 2 | 224 | 0 | 224 | 1.00 | (–) |
| 6 | 3 | 1,481 | 0 | 1,481 | 1.00 | (–) |
| 7 | 11 | 21,443 | 5 | 21,448 | 0.92 | (0.86–0.98) |
| 8 | 3 | 9,118 | 1 | 9,119 | 0.96 | (0.89–1.00) |
| 9 | 6 | 13,384 | 2 | 13,386 | 0.95 | (0.87–1.00) |
| Totals | 48 | 97,291 | 17 | 97,308 | 0.94 | (0.91–0.97) |

similar to the power of the test statistic for killer whales. There was insufficient information to test the influence of age on survival for either of these two species. However, there was sufficient information to test for differences in survival between sexes. For killer whales there was a significant effect ($P < 0.025$) with female survival being significantly greater than male survival; for white whales the effect was not significant (Table 6).

### *Longevity of Bottlenose Dolphins, Killer Whales, and White Whales*

For bottlenose dolphins, killer whales and white whales, the average number of days survived in captivity was 1,873.4 d (5.13 yr), 2,182.0 d (5.97 yr), and 2,026.9 d (5.54 yr), respectively. However, these statistics are of no real use in evaluating the husbandry record of the public display industry unless the entire cohort of animals that are used in estimating this statistic is dead. When this is not the case, this method of calculating longevity is very sensitive to the proportion of animals that have been recently acquired. In this study most of the animals included in the marine mammal inventory were not dead. Because

*Table 6.* Summary of average survival rate of killer whales and white whales by sex. Data are from National Marine Fisheries Service's Marine Mammal Inventory Report.

| | Days alive | Deaths | Average survival |
|---|---|---|---|
| Killer whales | | | |
| Male | 34,863 | 12 | 0.88 |
| Female | 52,366 | 6 | 0.96 |
| White whales | | | |
| Male | 42,482 | 6 | 0.95 |
| Female | 54,809 | 11 | 0.93 |

some animals have survived in captivity for over 30 yr, it is not possible to do a meaningful analysis of the data at this time with this statistic because of the limited number of animals that could be used in the analysis.

The expected number of years that an animal will survive, given that survival is constant from year to year, is estimated as follows (Seber 1973):

$$E\text{ (years to live)} = -1/\ln(\text{ASR})$$

In addition, this relationship is based on the assumption that survival is constant over all ages. Based on the average ASR for all animals of all three species reported in this study and assuming that this rate was constant, the expected number of years that an animal would survive in captivity is 14 yr. Based on the average survival rate for each species (Tables 1, 4, 5), estimates of species-specific life expectancies are 14 yr for bottlenose dolphins, 13 yr for killer whales, and 16 yr for white whales. For bottlenose dolphins, a non-calf that had been born in captivity would be expected to live an additional 33 yr. A free-ranging bottlenose dolphin having survived its first year in captivity would be expected to live an additional 19 yr. These estimates of life expectancy are all based on survival rates that are statistically indistinguishable. Because relatively small differences in the ASRs can result in large differences in estimates of life expectancy and because it is commonly accepted that at some point survival does start declining with age, we think that the ASR and not average longevity should be used in comparing the survival rate of free-ranging and captive dolphins or in comparing the survival rate of dolphins held at different institutions.

## Discussion

Unfortunately most of the published reports of dolphin mortality in captivity are not comparable to one another. Estimates of the average number of days or years survived (often referred to as longevity) are of little use in comparing husbandry practices, unless all of the animals in the analysis are dead or unless "longevity" is standardized against the maximum number of days that could have been survived. As an example, Greenwood and Taylor (1985) reported that the mean survival time of 9 killer whales that died in captivity was 2.21 yr, while the mean survival time of 15 animals still alive in captivity was 5.37 yr. The ASR based on the mean survival of the 9 dead animals is 0.64. The ASR based on the 15 animals still alive is 1.00, while the ASR for the entire sample of animals is 0.91. We encourage researchers to discontinue publishing the mean survival time of animals that have died in captivity, unless all of the animals acquired at a certain time have died and can be included in the analysis.

Furthermore, published estimates of dolphin mortality in captivity are often unweighted averages of annual survivorship, where sample sizes usually decrease over time (*see* Best and Ross 1984). This tends to weight the early years disproportionately. Because mortality in the first year of life or captivity may be higher than subsequent years (Bigg and Wolman 1975, Greenwood and Taylor 1985, results of this study), such an approach will produce negatively biased estimates of survival. For example, if a hypothetical sample of 12 animals were

*Table* 7. Hypothetical data set for comparing estimates of survival for captive dolphins.

| Animal # | Date acquired | Date of death | Animal-days survived | Deaths |
|---|---|---|---|---|
| 1 | 1-1-85 | 1-1-85 | 0 | 1 |
| 2 | 1-1-85 | 7-1-85 | 180 | 1 |
| 3 | 1-1-85 | 2-1-86 | 395 | 1 |
| 4 | 1-1-85 | 8-1-86 | 576 | 1 |
| 5 | 1-1-85 | 3-1-87 | 788 | 1 |
| 6 | 1-1-85 | 9-1-87 | 972 | 1 |
| 7 | 1-1-85 | 4-1-88 | 1,185 | 1 |
| 8 | 1-1-85 | 10-1-88 | 1,368 | 1 |
| 9 | 1-1-85 | 5-1-89 | 1,580 | 1 |
| 10 | 1-1-85 | 11-1-89 | 1,764 | 1 |
| 11 | 1-1-85 | 6-1-90 | 1,976 | 1 |
| 12 | 1-1-85 | 12-1-90 | 2,159 | 1 |
| Totals | | | 12,943 | 12 |
| Annual Survival rate = 0.71 | | | | |
| Number of animal-years = 42 | | | | |
| Number of animal-years survived = 30 | | | | |
| Annual Survival rate = 0.71 | | | | |

all captured on 1 January 1985 and survived as shown in Table 7, the actual survivorship based on the procedure recommended in this paper or an analysis of animal-years survived/total animal-years is 0.71. However, if the 6 yr of annual survival are averaged, the resulting estimate is only 0.41. In general, estimates of captive survival should be weighted by either animal-days or animal-years.

Also, estimates of survival from date of capture to the present are somewhat misleading (*see* Walker 1975) because they also incorporate survival data over years, during which survival rates may have changed. For example, Walker (1975) reported that 50% of bottlenose dolphins captured between 1966 and 1972 survived the initial two year period. The annual survival estimate for these data is 0.71 (data are from Walker 1975, table 4); the survival rate given an animal survived the first year is 0.79. We recommend that estimates of captive survival be based on annual estimates of survival and that factors such as acclimation period be considered in comparing husbandry practices.

Finally, various researchers have estimated survival in captivity based on what Bigg (1982) referred to as animal-years (*see* Hui and Ridgway 1978, Best and Ross 1984). As demonstrated in Table 7, estimates of survival based on animal-years and animal-days should be identical. However, it is necessary in using animal-years to prorate partial years, where an animal may have died mid-year or where the reporting period ended. We recommend authors specify how this proration was accomplished to facilitate the comparison of survival rates between studies.

Ohsumi (1979) reported that existing data were not suitable to estimate the natural rate of mortality for bottlenose dolphins and killer whales. He further reported that the annual mortality rate of free-ranging white whales was 0.06. However, this latter figure is actually the percent calves in the population 8 mo after the peak of calving (*see* Sergeant 1973, p. 1089), and is not a valid estimate of annual mortality. Sergeant (1973) suggested a mortality rate of 0.10 for newborn calves between months 1 and 6. Based on a regression analysis, Ohsumi predicted that the annual mortality rate of bottlenose dolphins, killer whales and white whales would be 0.13, 0.09 and 0.12, respectively. In this analysis of survival in captivity, mortality rates for these same three species were 0.07, 0.07 and 0.06, which indicates that survival in captivity may be better than or equal to survival in the wild. The only published report of mortality rates in the wild for any of these three species is for killer whales off Vancouver Island, British Columbia, Canada (Bigg 1982), where 11 deaths occurred over 637 animal-years for an annual rate of mortality of 0.02; the 95% confidence interval is 0.01–0.03 (calculated by DPD based on data from Bigg 1982). This rate includes data from juveniles (27% of animal-years), adult males (28%), and adult females (45%). These data indicate that, at least for killer whales, survival in captivity may be less than survival off Vancouver Island, British Columbia.

Until additional studies are completed, it will not be possible to compare the survivability of free-ranging animals for these three species with captive animals. One reviewer noted that the average age of captured animals is generally less than the average age of free-ranging animals. Therefore, in comparing survival of captive and free-ranging animals, the effect of age composition on average survival may be important.

Indirect comparison of the survival rate of captive animals to free-ranging animals is possible by computing the mortality rate needed to give a stable population, given estimates of reproductive rates. Reilly and Barlow (1986) cite an example for free-ranging bottlenose dolphins with a 12-yr age of attainment of sexual maturity and a 2 to 4 yr calving interval. Given these reproductive rates and assuming the population is stable, adult survival rates must be between 0.92 and 0.95 (Reilly and Barlow 1986, fig. 4). This range of survival rates is consistent with the rates estimated for captive animals.

Sergeant (1973) and Jones (1982) reported that the maximum reported longevity for bottlenose dolphins in captivity is 25 yr. The maximum reported longevity in the Marine Mammal Inventory was 28 yr. As previously mentioned, we do not feel this statistic is particularly informative for the purposes of comparing husbandry practices.

Best and Ross (1984) reported that bottlenose dolphins caught in South African waters and maintained in captivity survived at an average rate of 0.87, given they survived the first year. These data cover the years 1961 through 1982. They further noted that first year survival was low (0.58). The 0.87 survival rate does not include 9 animal-years for a single animal that survived 19 yr in captivity. If these data are included, the (unweighted) annual survival rate is 0.92, while the survival rate, weighted by animal-years, is 0.86. We feel the weighted estimate of survival is a better representation of the data.

*Table 8.* Recalculated previously published survival rates for killer whales.

| | Years survived | Total years | Survival rate |
|---|---|---|---|
| Bigg and Wolman (1975) | 118 | 139 | 0.85 |
| Hui and Ridgway (1978) | 134.47 | 151.47 | 0.89 |

Reynolds (1987) reported that the average survival rate of bottlenose dolphins maintained in captivity in the southeastern U.S. was 0.86 ± 0.04. He further noted that survival was independent of facility, but was affected by the area in which animals were originally captured. The survival rates reported in Best and Ross (1984) and Reynolds (1987), are significantly less than the rate of survival reported in this study. In addition, Klinowska and Brown (unpublished manuscript prepared for the Department of Environment, U.K. 1986) reported survival rates for captive bottlenose dolphins in the U.K. that were also significantly lower than those reported here. However, the range of survival rates for individual institutions is similar for all the above reports. The reason(s) for the observed difference in average survival is (are) not clear at this time.

For killer whales, reported rates of captive survival vary from 0.50 for adults and 0.89 for immatures (data are from Bigg and Wolman 1975) to 0.95 for adults and immatures combined (Hui and Ridgway 1978). Data from the former study are through April 1974 and for the latter study through May 1976. Hui and Ridgway (1978) did not account for the entire animal-year in those years in which deaths occurred and may have assumed that animals survived all of 1976, even though data are provided only through May. Given the data provided by Hui and Ridgway (1978) in their table 1, survival estimates were recalculated based on the methods presented in this paper. In addition, data on the survival of adults and immatures from Bigg and Wolman (1975) were pooled because of the relatively small number of adults in their sample. The results of this reanalysis are presented in Table 8.

These rates are not significantly different, although they are slightly lower than the average rate reported in this study. If the one stillborn animal included in the data reported by Hui and Ridgway is excluded from the analysis, the resulting survival rate is 0.91, which is not significantly different from our results. Furthermore, Hui and Ridgway (1978) reported that adult male survival was greater than the survival rate of adult females. The opposite was reported in this study. Klinowska and Brown (unpublished manuscript prepared for the Department of the Environment, U.K. 1986) reported an average annual survival rate of 0.89 for captive killer whales in the U.K. This rate of survival was not significantly different from our results.

At this time it is not possible to compare the survivability of animals in captivity with that of animals in the wild. It is clear that differences between institutions exist. Additional data from free-ranging animals are needed to determine if captive animals have similar life expectancies. From our review of the literature, we strongly recommend that data concerning captive survival of cetaceans be reported such that it includes the acquisition date, date of death, reporting date for animals still alive, the age-class of an animal, and its sex. In addition, because estimates of longevity are extremely sensitive to small differences in survival, we recommend that this parameter not be used in comparing the survival rates of captive or free-ranging cetaceans. Also, the data reported here indicate that the survival rate of the three species of captive cetaceans referred to in this study is generally between 0.90 and 0.95. Rates of survival above this range are indicative of superior husbandry practices; survival rates below this range indicate that there may be room for improvement. Additional information is needed on how the area of capture influences rates of survival. Finally, in comparing survivability, age composition must be considered. Additional work is needed to investigate the importance of how mortality patterns change with age.

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## Literature Cited

Bart, J., and D. S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63:1078–1090.

Best, P. B., and G. J. B. Ross. 1984. Live-capture fishery for small cetaceans in South African waters. Report of the International Whaling Commission 34:615–618.

Bigg, M. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Report of the International Whaling Commission 32: 655–666.

Bigg, M. A., and A. A. Wolman. 1975. Live-capture killer whale (*Orcinus orca*) fishery, British Columbia and Washington, 1962–73. Journal of the Fisheries Research Board of Canada 32:1213–1221.

Duffield, D., and N. Dimeo-Ediger. 1984. Marine mammals in captivity: Census and significance. Whalewatcher 18(4):14–15.

Freund, J. E. 1971. Mathematical statistics. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Greenwood, A. G., and D. C. Taylor. 1985. Captive killer whales in Europe. Aquatic Mammals 1:10–12.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hui, C. A., and S. H. Ridgway. 1978. Survivorship patterns in captive killer whales (*Orcinus orca*). Bulletin of the Southern California Academy of Sciences 77:45–51.

Jones, M. L. 1982. Longevity of captive mammals. Zoological Garten 52(2):113–128.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

OHSUMI, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the southern hemisphere minke whale. Report of the International Whaling Commission 29:397–406.

POOLE, L., M. BORCHERS AND D. M. CASTLEWITZ. 1981. Some common BASIC programs: Apple II edition. Osborne/McGraw Hill, Berkeley, California.

REILLY, S. B., AND J. P. BARLOW. 1986. Rates of increase in dolphin population size. Fisheries Bulletin 84:527–533.

REYNOLDS, J. E. 1987. Identification and evaluation of possible differences in hardiness of bottlenose dolphins from different coastal areas of the southeastern United States. Final Report to the U.S. Marine Mammal Commission MM2324822-1. 24 pp.

SEBER, G. A. F. 1973. The estimation of animal abundance. Hafner Press, New York, New York.

SERGEANT, D. E. 1973. Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. Journal of the Fisheries Research Board of Canada 30:1065–1090.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State University Press, Ames, Iowa.

TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. Journal of Wildlife Management 38:459–472.

WALKER, W. A. 1975. Review of the live-capture fishery for smaller cetaceans taken in southern California waters for public display, 1966–1973. Journal of the Fisheries Research Board of Canada 32:1197–1211.

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# A New Genus and Species of Prosobranch Gastropod (?Fasciolariidae) from the Mariana Islands

by

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*Abstract.* A new genus and species of prosobranch gastropod, ***Falsilatirus pacificus,*** is described from deep water off Arakane Reef, in the Northern Mariana Islands. The questionable placement of this new species in the family Fasciolariidae is based on shell characters owing to the unavailability of soft parts for study.

## INTRODUCTION

Deepwater shrimp trapping operations were conducted from 1982 to 1984 by the National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory as part of their Resource Assessment Investigation of the Mariana Archipelago (RAIOMA) program. Incidental catches in these operations included shells of several gastropod mollusks (D. B. Smith and R. B. Moffitt, unpublished data). Some of these mollusks were collected alive, but most were carried into baited traps by hermit crabs of the genus *Trizopagurus.* Among these transported shells were three crabbed specimens of a distinctive new genus and species of prosobranch gastropod that is described herein as ***Falsilatirus pacificus*** and tentatively placed in the Fasciolariidae.

## SYSTEMATIC ACCOUNT

### Family Fasciolariidae Gray, 1847

### *Falsilatirus* Emerson & Moffitt, gen. nov.

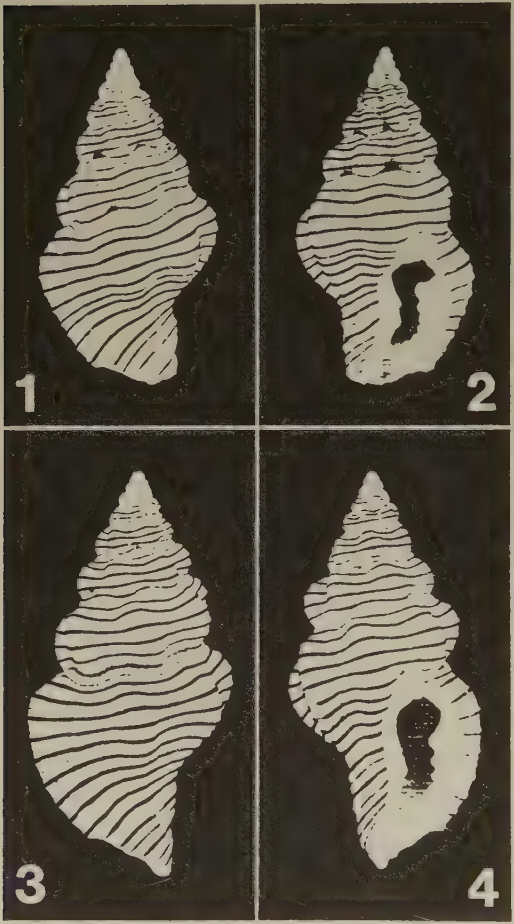
Type species: ***Falsilatirus pacificus*** Emerson & Moffitt, sp. nov.

**Diagnosis:** Shell in general shape and coloration somewhat resembles certain of the finely lirate *Latirus* Montfort, 1810, type species: *L. gibbulus* (Gmelin, 1791). Differs from the known fasciolariid genera in having distinctive labial and columellar dentition and by having a recurved siphonal canal. See description of the type species.

### *Falsilatirus pacificus* Emerson & Moffitt, sp. nov.

(Figures 1–4)

**Description:** Shell angulate fusiform, solid and attaining 7½ postnuclear whorls (embryonic whorls not preserved) and 42+ mm in length. Post-embryonic whorls strongly axially ribbed, with 5 elongate nodules on the body whorl. Surface colored pale buff and ornamented with conspicuous, dark brown, evenly spaced spiral cords throughout. Midportion of whorls encircled with a paler, whitish band. Whorls of the spire with 3 or 4 dark brown, primary spiral cords; body whorl with 12 primary cords, extending from the suture to near the base. Interspaces between the primary spiral cords sculptured with a minor pale brown cord medially placed between 3 or 4 spiral lirations. Aperture white, prominently dentate with an open anal groove and a recurved siphonal canal (anterior portion lost to breakage). Outer lip with a submarginal, shelflike projection armed with 6 semifused denticles, the largest positioned posteriorly. Columella with a slightly raised outer margin



Explanation of Figures 1 to 4

Figures 1–4. Type specimens of ***Falsilatirus pacificus*** Emerson & Moffitt, sp. nov. Figures 1, 2: paratype a. Figures 3, 4: holotype. All figures ×1.5.

and with 2 denticle-like plicae, the anterior one forming a major fold. Radula and soft parts not seen.

Measurements in mm, holotype: 41.67 in length, 20.84 in width (Figures 3, 4); paratype a: 35.86 in length, 19.32 in width (Figures 1, 2); paratype b: 31.25 in length, 16.26 in width.

**Type locality:** Off Arakane Reef, Northern Mariana Islands, 15°38.4′N, 142°46.2′E, in 123–503 m (67–275 fathoms), NOAA ship *Townsend Cromwell*, cruise TC 83-05, station 167, taken in shrimp traps, 19 December 1983.

**Distribution:** Known only from the type locality.

**Type depository:** Holotype, American Museum of Natural History (AMNH), no. 225996; paratype a, United States National Museum, no. 859320; paratype b, AMNH no. 225997.

**Remarks:** As mentioned above, these specimens, which lack preserved embryonic whorls, suggest the fasciolariid genus *Latirus*, especially from the dorsal aspect and by the presence of a prominent spiral columellar fold. For example, see *Latirus angulatus* (RÖDING, 1798:118; BULLOCK, 1974:figs. 16–21) from the western Atlantic and *L. filosus* (SCHUBERT & WAGNER, 1829:100, pl. 227, figs. 4019, 4020; ABBOTT & DANCE, 1982:184, illus.) from west Africa. The known latiroid species, however, have a nonrecurved siphonal canal and mostly lack denticles inside the outer lip. In the buccinid subfamily Pisaniinae Gray, 1857, many taxa possess shells with denticulate outer lips (subfamily reviewed by CERNOHORSKY, 1971, 1975), but generally lack a spiral ridge on the parietal wall. See especially *Clivipollia pulchra* (REEVE, 1846, *Ricinula*, no. 20, pl. 3, figs. 20a, b; PONDER, 1972:264, pl. 25, fig. 4; ABBOTT & DANCE, 1982:172, illus.) from the western Pacific. On the bases of shell characters alone, data are not sufficient for unequivocal assignment to either the Fasciolariidae or Buccinidae. We have tentatively referred this new genus and species to the former family, owing largely to the presence of a distinctive columellar fold. Final familial placement must await the acquisition and study of the radula and soft parts of this new taxon.

## ACKNOWLEDGMENTS

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## LITERATURE CITED

ABBOTT, R. T. & S. P. DANCE. 1982. Compendium of seashells. E. P. Dutton, Inc.: New York. 411 pp.

BULLOCK, R. C. 1974. A contribution to the systematics of some West Indian *Latirus* (Gastropoda: Fasciolariidae). Nautilus 88(3):69–79.

CERNOHORSKY, W. O. 1971. Indo-Pacific Pisaniinae (Mollusca: Gastropoda) and related buccinid genera. Rec. Auckland Institute & Museum 8:137–167.

CERNOHORSKY, W. O. 1975. Supplementary notes on the taxonomy of buccinid species of the subfamily Pisaniinae (Mollusca: Gastropoda). Rec. Auckland Institute & Museum 12: 175–211.

GRAY, J. E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. Proc. Zool. Soc. Lond., for 1847: part 15, nos. 178–179, pp. 129–219.

GRAY, J. E. 1857. Guide to the systematic distribution of Mollusca in the British Museum. Part 1. London. i–xii + 230 pp.

Monfort, P. D. de. 1810. Conchyliologie systématique et classification méthodique des coquilles. . . . Paris. Vol. 2:676 pp.

Ponder, W. F. 1972. Notes on some species and genera of the family Buccinidae (Neogastropoda). Jour. Malacol. Soc. Australia 2(3):249–265.

Reeve, L. 1846. Conchologia Iconica: illustrations of the shells of molluscous animals. Monograph of the genus *Ricinula*. London. Vol. 3, text and 6 pls.

Röding, P. F. 1798. Museum Boltenianum . . . : pars secunda continens Conchylia. . . . J. C. Trappii: Hamburg. Pp. i–viii + 199.

Schubert, G. M. & J. A. Wagner. 1829. Systematisches Conchylien-Cabinet von Martini und Chemnitz, neu herausgegeben. . . . Nürnberg. Vol. 12, *Turbinella*, pp. 98–104, pl. 227.

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# Surface Manifestations of Subsurface Thermal Structure in the California Current

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**Remote sensing is useful for studying certain oceanographic problems only if the signal obtained from the sea surface contains information about subsurface structure. Historical bottle temperature data from the California Current were analyzed for surface manifestations of vertical structure and subsurface mesoscale structure. Results showed that surface temperature is useful in predicting thermocline strength over a large area south of Point Conception: the error of a regression estimate is 20–30% less than the error of the seasonal mean. However, surface temperature gives little useful information about mixed layer depth. Mesoscale patterns of temperature at the surface and at depth (caused by eddies, meanders and upwelling) are coherent ($r^2 > 0.50$) to a depth below the mixed layer only off central California and Point Conception and along the coast of Baja California. Coherence is most likely to extend below the mixed layer during summer, when the water column is strongly stratified and the mixed layer is most shallow. Thus some aspects of subsurface structure, within limited regions of the California Current, have surface manifestations potentially detectable by satellite sensors.**

## 1. INTRODUCTION

Satellite sensors have revolutionized oceanography in the past decade by providing repetitive and synoptic measurements of temperature, color, winds, and currents over large areas of the sea surface. Sea truth validation of satellite estimates of surface parameters has led to sensor and algorithm refinements that have reduced errors to acceptable levels for many applications. However, for studies of structure and processes below the sea surface, even error-free satellite data are useful only if the surface signal contains information about subsurface structure. For example, in an expendable bathythermograph (XBT) survey across the central north Atlantic [*Dugan* 1980], an unambiguous surface temperature signal was detected for only one of four cold-core eddies observed in the permanent thermocline. A thermocline front had no corresponding surface temperature signal, while a surface thermal front did not extend into the thermocline. From a global survey of sea surface temperature (SST) fronts detected by satellite, *Legeckis* [1978] concluded that isothermal surface layers obscure subsurface horizontal temperature gradients in tropical oceans year-round and in subtropical oceans during summer.

Satellite infrared temperature data have been used increasingly in studies of the California Current system as the importance of mesoscale variability has become more apparent [*Bernstein et al.*, 1976; *Koblinsky et al.*, 1984; *Flament et al.*, 1985]. Above 500 m, this system consists of (1) a broad equatorward California Current with a low-salinity core about 400 km offshore, (2) a poleward California Undercurrent with a core at ~300-m depth over the continental slope, and (3) a fall-winter poleward California Countercurrent at the surface within 150 km of the coast [*Simpson et al.*, 1986]. Mesoscale coastal jets or streamers and offshore eddies are much more energetic than the large-scale mean surface flows, as is generally true in eastern boundary currents [*Wyrtki et al.*, 1976].

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has sampled standard depths at stations covering most of the California Current system since 1950 (Figure 1). Gross vertical structure parameters such as mixed layer depth, thermocline depth, and stratification or stability can be derived from CalCOFI temperature data. Although the 37- to 74-km spacing of CalCOFI stations may barely resolve mesoscale eddies, meanders in the core of the California Current, and coastal upwelling, such features are clearly visible in maps of cruise data [*Wyllie*, 1966].

In this paper I analyze a large set of CalCOFI hydrographic data to answer two basic questions about the utility of remotely sensed surface data in the California Current: (1) Can information about vertical structure below the surface be derived from surface temperature? (2) Are mesoscale patterns of surface temperature coherent with patterns below the mixed layer or thermocline?

Surface data will be considered useful in estimating subsurface structure (question 1) if they can produce an estimate that is more precise than an estimate based on climatology alone (i.e., if the standard error of the regression estimate is less than the standard deviation around annual or seasonal station means). Vertical coherence of mesoscale patterns (question 2) was examined within regions with dimensions of 100–400 km to exclude larger-scale latitudinal and onshore-offshore patterns. Variability of temperature at standard depths within regions represents effects of offshore eddies, California Current meanders, coastal upwelling, and other structures and processes resolved by the station grid. Correlation between the surface and depth is a measure of the coherence of mesoscale surface structure with depth. Alternatively, it is a measure of the contribution of subsurface structure to the surface temperature signal.

The practical utility of estimates of subsurface structure derived from surface observations will depend on the particular problem at hand. This empirical analysis is intended to explore the potential and limitations of extrapolating accurate remotely sensed surface data into the water column. Errors introduced into the surface signal at the air-water interface, in the atmosphere, and by the sensor are not considered here.

## 2. METHODS

The CalCOFI data set includes temperature at 14 standard depths (0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, and

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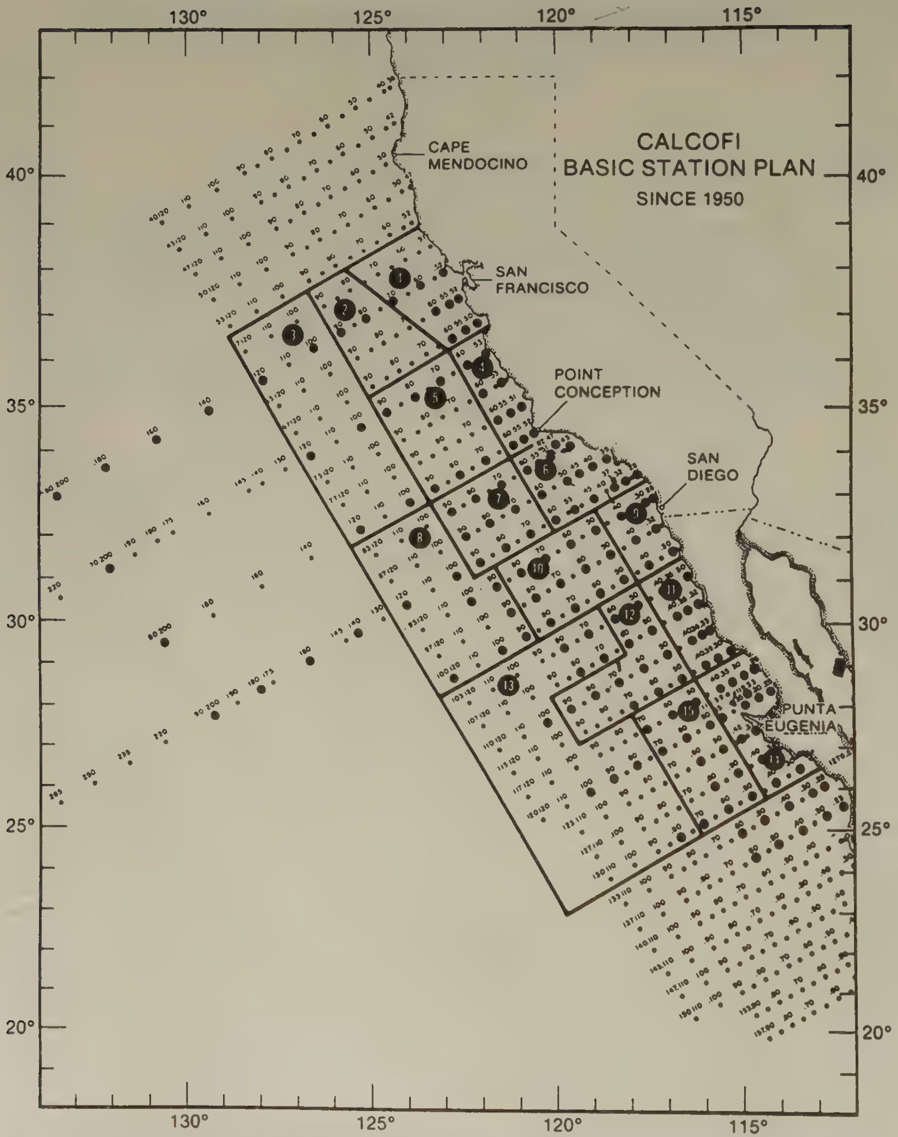

Fig. 1. CalCOFI station grid. Only the most frequently sampled stations (large dots) on cardinal lines 60, 70, 80, 90, 100, 110, 120, and 130, out to station 120, were used in the verical structure analysis. Regions for the correlation analysis are named as follows: 1, central California coastal; 2, central California transition; 3, central California oceanic; 4, Point Conception coastal; 5, Point Conception transition; 6, southern California coastal; 7, southern California transition; 8, southern California oceanic; 9, border coastal; 10, border transition; 11, northern Baja California coastal; 12, northern Baja California transition; 13, northern Baja California oceanic; 14, Punta Eugenia coastal; 15, Punta Eugenia transition.

500 m) from subsets of the basic station grid (Figure 1) occupied on 200 cruises from February 1950 to October 1984 (7–231 stations per cruise).

### 2.1. *Vertical Structure*

Three vertical structure parameters were estimated from discrete temperature profiles. Thermocline strength ($|\Delta T/\Delta z|$) was calculated in the depth interval with the maximum vertical temperature gradient. Location of the thermocline depth within this interval was weighted by the temperature gradients above and below the interval. Mixed layer depth was calculated as the depth at which temperature extrapolated from the apparent thermocline equaled surface temperature [*Wyrtki,* 1971]. Thus mixed layer depth is always less than the thermocline depth.

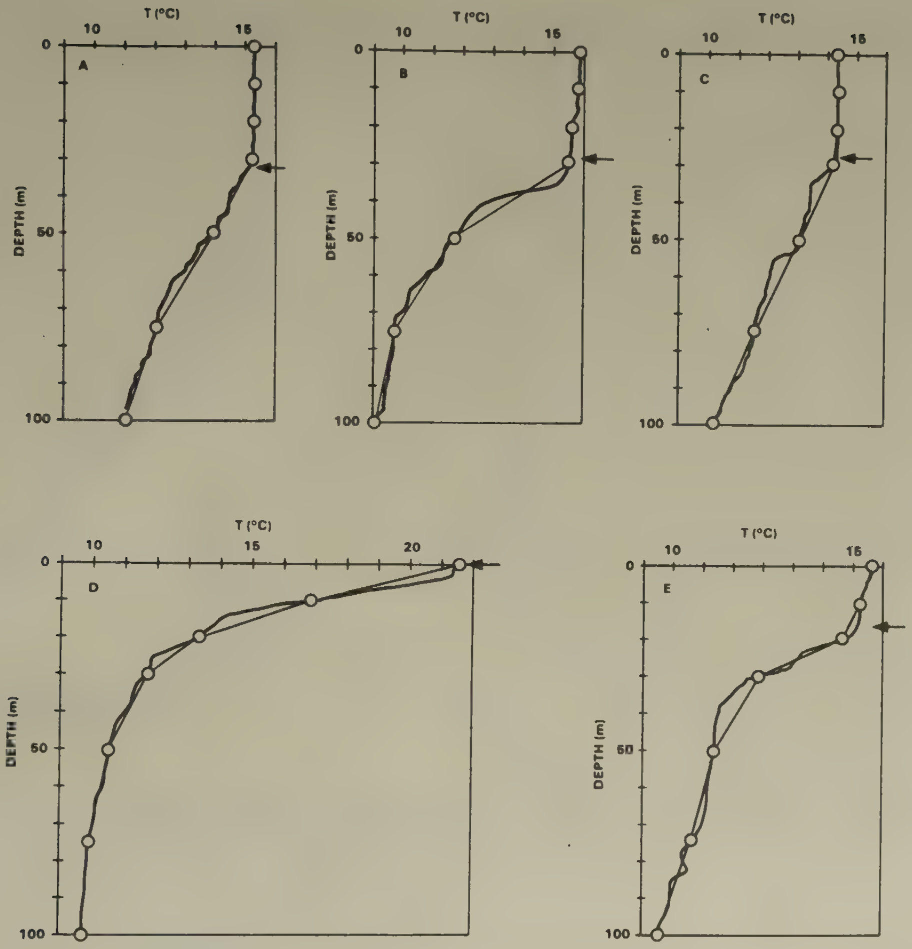

Fig. 2. A variety of CTD temperature profiles from the Southern California coastal region (Figure 1) compared to the profiles that would be observed with standard CalCOFI bottle samples at 0, 10, 20, 30, 50, 75, and 100 m. Mixed layer depths (arrows) are calculated from the discrete profiles as described in the text. CTD data were provided by R. Lynn.

CalCOFI bottle samples cannot completely describe the vertical structure seen in continuous temperature profiles (Figure 2). Thermocline strength is underestimated (e.g., Figure 2*b*). Finescale features such as steps and inversions are not resolved (Figures 2*c* and 2*e*). Mixed layer depth may be estimated accurately (Figures 2*a* and 2*c*) or not (Figure 2*b*). About 10% of the stations, for which the bottle data gave a mixed layer depth of ≤0 m (Figure 2*d*) or a thermocline in the deepest interval of the cast were considered to be inadequately described by bottle samples and were omitted from the analysis.

Linear regression relationships between surface temperature and vertical structure parameters were calculated at 68 cardinal stations occupied >20 times (Figure 1). Utility of the relationships was measured by ratios of the rms error about the regression line to the standard deviation and to the mean of the dependent variable. The first ratio will be called the relative rms error. For large $n$, as in this analysis, the relative rms error is equal to the square root of the ratio of the residual sum of squares to the total sum of squares, or the square root of $(1 - r^2)$. The second ratio (rms error/mean) is a coefficient of error, or residual variation, analogous to the coefficient of variation.

### 2.2. *Vertical Coherence of Mesoscale Structure*

Mesoscale regions are delimited in Figure 1. The alongshore boundaries roughly define a transition zone between coastal and oceanic domains [*Simpson et al.*, 1986]. Regional correlations of temperature at 0 m and at depth were calculated from sums of squares within cruises to eliminate variance and covariance between cruises (seasonal and interannual variability). Decorrelation depth is defined as the depth at which correlation with the surface equals 0.71 ($r^2$=0.50), calculated by linear interpolation between standard depths. Mean thermocline depth and mixed layer depth, as defined above, were calculated for each region and season. Differences between decorrelation depth and mixed layer

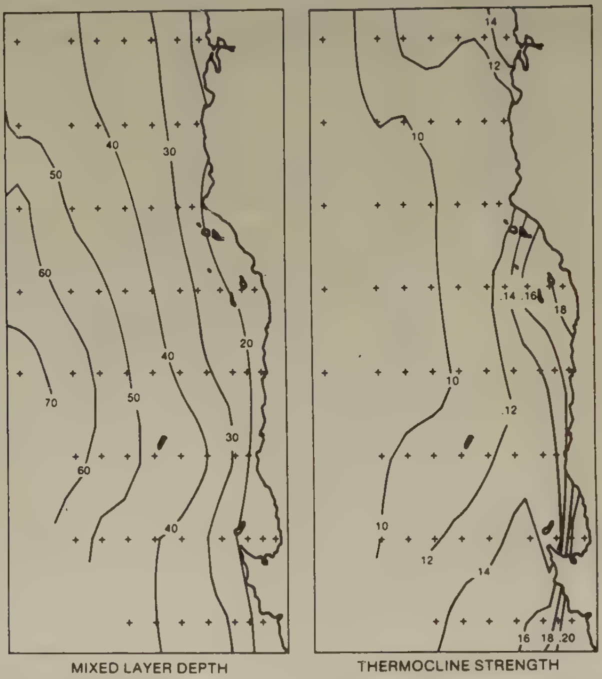

Fig. 3. Mean mixed layer depth (in meters) and thermocline strength (in degrees Celsius per meter) at 68 CalCOFI cardinal stations off California and Baja California, 1950–1984.

or thermocline depth were tested by the $t$-test [*Sokal and Rohlf*, 1969] using the null hypothesis that $r=0.71$ at the mixed layer or thermocline depth.

## 3. RESULTS

### 3.1. *Vertical Structure*

The mean mixed layer deepens and the thermocline weakens from nearshore to offshore stations (Figure 3). Mixed layer and thermocline depths are strongly correlated (Figure 4, $r=0.933$, $n=6144$). The steplike distribution of points in the scatter plot is an artifact of the discrete bottle spacing. Both features are most shallow nearshore between Point Conception and Punta Eugenia and are correlated with thermocline strength ($r=-0.34$ for mixed layer depth and $r=-0.43$ for thermocline depth). The thermocline is strongest in two nearshore areas: the Southern California Bight and south of Punta Eugenia.

Since mixed layer depth and thermocline depth are so closely related, only mixed layer depth and thermocline strength were considered as functions of surface temperature. Regressions of these two vertical structure parameters on surface temperature are summarized in Table 1. Overall regression relationships are statistically significant ($P[r=0] \ll 0.001$ by the $F$-test; Figure 5). For both parameters, $r^2$ calculated within stations is greater than the overall value. $R^2$ calculated within stations and seasons is less than the overall value, perhaps because of small ranges of the independent variable at some stations in some seasons.

Spatial patterns of relative rms error about the seasonal station regression lines are illustrated in Figure 6. Regression on surface temperature gives an estimate of mixed layer depth with less error than that of the seasonal mean only in a small region offshore of Punta Eugenia. Regression on surface temperature gives an estimate of thermocline strength with an error 20–30% less than that of the seasonal mean in a large area south of Point Conception. The coefficient of error (rms error/mean) of the estimates at these 50 southern stations is 0.34 (±0.27). North of Point Conception and at the offshore edge of the station grid, the regression estimate of thermocline strength is no more precise than the seasonal mean at a station.

### 3.2. *Vertical Coherence of Mesoscale Structure*

Profiles of the correlation of surface temperature with temperature at depth in coastal, transition, and oceanic regions are shown in Figure 7. The decorrelation depth ($r^2=0.50$) is often significantly deeper than the mixed layer in regions off central California and Point Conception and in coastal regions off Baja California (Table 2). The decorrelation depth is most likely to be deeper than the mixed layer in summer, when the water column is strongly stratified and the mixed layer is most shallow. In contrast, the decorrelation depth tends to be significantly more shallow than the mixed layer in regions offshore of Baja California, where the mixed layer is deepest. Among 15 regions and 4 seasons (60 cases), the decorrelation depth is deeper than the mixed layer in 26 cases ($r=0.83\pm0.04$ at the mixed layer depth), not significantly different in 23 cases ($r=0.71\pm0.04$), and more shallow in 11 cases ($r=0.55\pm0.04$).

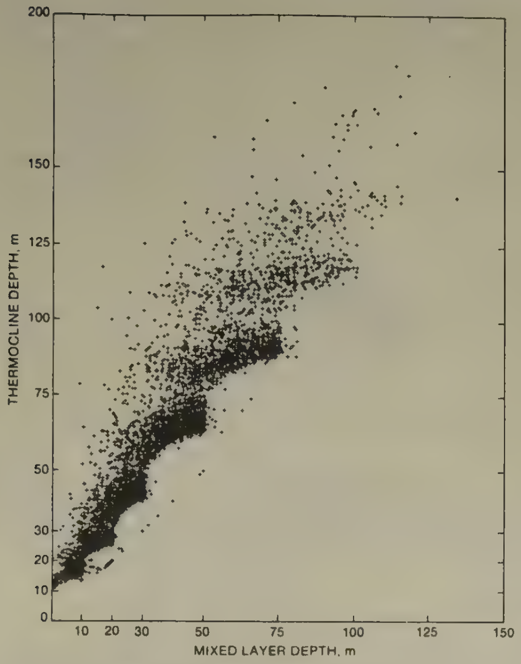

Fig. 4. Thermocline depth versus mixed layer depth at 68 CalCOFI cardinal stations, 1950–1984.

## 4. Discussion

### 4.1. *Vertical Structure*

In the CalCOFI data set, mixed layer depth cannot be derived from surface temperature by linear regression; the deepest mixed layers are found at stations with intermediate surface temperatures (Figure 5). Shoaling of the thermocline can be associated with either warming or cooling by (1) seasonal warming and stratification of the surface layer or (2) upwelling of colder, deeper water caused by offshore transport of warm surface water. In either case, shoaling will occur when winds are too weak to produce enough vertical shear to overcome stratification at the bottom of the mixed layer. Upwelling is a coastal, spring-summer phenomenon, and seasonal warming peaks in late summer or early fall. It should be possible to separate these effects using season- and station-specific regressions, but the results summarized in Table 1 show that on average, there is no gain in precision ($r^2$ decreases when calculated within stations and seasons).

Figure 8 illustrates relationships at CalCOFI station 90.70, located ~300 km west of San Diego. Although the station is beyond the immediate influence of coastal upwelling, the regression of mixed layer depth on surface temperature is significant only for summer ($r^2 = 0.21$). Mean summer mixed layer depth is 31.2 m with a standard error of 14.0 m, while the rms error about the regression line is 12.6 m, only 10% less than the standard error. An exceptionally large improvement is realized at station 120.90: in summer, mean mixed layer depth is 37.6 m with a standard error of 22.7 m, while the regression rms error is 14.0 m, an improvement of 38%. Generally, however, surface temperature does not give useful information about mixed layer depth even using regression relationships specific for each season at each station.

In contrast to mixed layer depth, thermocline strength is strongly related to surface temperature (Figures 5 and 6, Table 1), because thermocline strength is essentially the difference between the temperature of the surface layer and the relatively constant temperature of the deep layer below the seasonal thermocline. At station 90.70 (Figure 8), regressions for winter, spring, and summer are significant ($r^2 = 0.34$, 0.27, and 0.33, respectively). While mean spring surface temperature (14.55°C) is only slightly less than mean winter surface temperature (14.69°C), the regression intercepts are different: at the same temperature, thermocline strength in winter is 20% greater than thermocline strength in spring. This illustrates the value of season-specific regressions. In fall, regression between thermocline strength and surface temperature is not significant. Very large thermocline gradients exist without a rise in surface temperature.

South of Point Conception and within 300–500 km of the coast, regression on surface temperature gives an estimate of thermocline strength that is 20–40% more precise than an estimate equal to the seasonal mean. For example, at station 110.70, summer thermocline strength estimated from the climatological mean is 0.109 ± 0.040°C m$^{-1}$. From an observed surface temperature of 19.0°C (0.4°C above the mean), one could estimate with equal confidence that the thermocline strength is 0.166 + 0.029°C m$^{-1}$.

Thermocline strength is most strongly related to surface temperature in the Southern California Bight, in shallow coastal waters north and south of Punta Eugenia, and in a band parallel to the coast ~200 km off Punta Eugenia (areas within the 0.70 contour of relative rms error, Figure 6). Circulation in the Southern California Bight is dominated by the semiclosed southern California eddy. Bahia Sebastian Vizcaino, to the north of Punta Eugenia, is likewise isolated from the large-scale flow of the California Current and Inshore Countercurrent. Thus local forcing at the surface may have a greater effect on subsurface structure in these coastal regions. The band offshore of Punta Eugenia is characterized by complex meanders in the core of the California Current and a recurrent anticyclonic eddy near Guadalupe Island [*Lynn et al.*, 1982]. Attenuation of the California Current may increase the relative impact of local forcing in this region as well.

### 4.2. *Vertical Coherence of Mesoscale Structure*

Temperature patterns at depths below the mixed layer are coherent with surface temperature patterns ($r^2 > 0.50$) in coastal, transition, and oceanic regions off central California and Point Conception and in coastal regions off northern Baja California and Punta Eugenia (Table 2). Coherence to a depth below the mixed layer occurs most frequently in regions with shallow mixed layers, but it occasionally occurs in oceanic regions with deeper mixed

TABLE 1. $R^2$ Values for Linear Regressions on Surface Temperature

| | Mixed Layer Depth | Thermocline Strength |
|---|---|---|
| Overall | 0.024 | 0.200 |
| Within stations | 0.153 | 0.267 |
| Within stations and seasons | 0.005 | 0.102 |

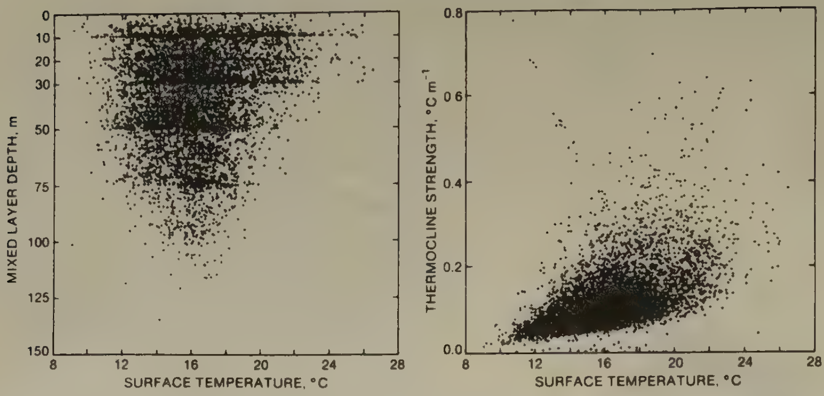

Fig. 5. (Left) mixed layer depth versus surface temperature and (right) thermocline strength versus surface temperature at 68 CalCOFI cardinal stations, 1950–1968.

layers. In other cases, $r^2$ falls below 0.50 within the mixed layer and to a value as low as 0.24 at the mixed layer depth.

Correlation is a simple way to compare surface and subsurface patterns, but may underestimate the value of surface patterns as manifestations of subsurface structure. For example, *Simpson et al.* [1984] used sea surface temperature imagery in a study of a three-layer eddy in the transition zone off Point Conception. The subsurface warm-core eddy was clearly manifested as a warm

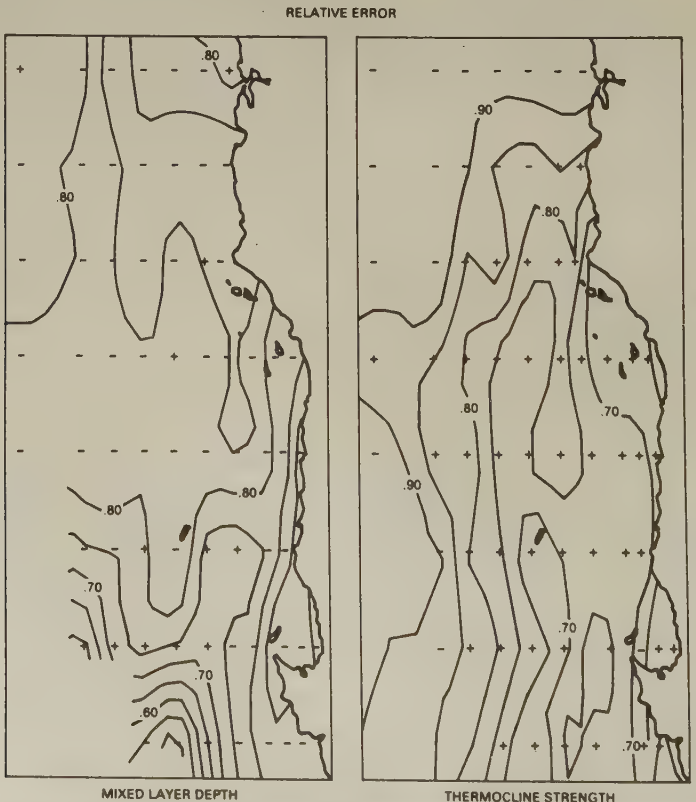

Fig. 6. Relative rms error of estimates of mixed layer depth and thermocline strength from regression on surface temperature (plus signs) or from the seasonal station mean (minus signs, where the regression estimate is no more precise than the seasonal mean).

patch at the surface, but there was a cold-core layer at 75–175 m between the eddy and the warm surface layer. Although the anticyclonic flow of the eddy was coherent to ~1000 m, correlation with the surface temperature pattern dropped to zero in the cold-core layer [*Simpson et al.*, 1986].

Surface-subsurface temperature correlation profiles show two basic patterns in the CalCOFI data set: (1) a monotonic decrease of $r$ with depth or (2) a minimum $r$ at an intermediate depth between 50 and 125 m (Figure 7). Correlation minima occur year-round at 50–75 m in the southern California coastal region and in spring, summer, and fall at 75–125 m in the border coastal region. These correlation minima occur below the thermocline, the strength of which is very strongly related to surface temperature in the

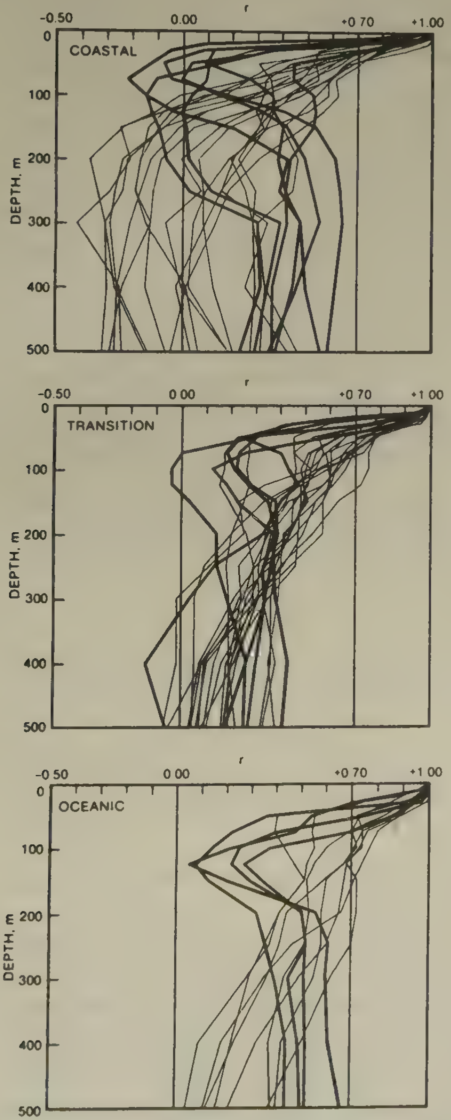

Fig. 7. Temperature correlation profiles (correlation of surface temperature with temperature at depth, within cruises), by region and season, from 1950–1984 CalCOFI data. Heavy lines are profiles with a minumum $r$ value that is significantly less than at least one $r$ value at a greater depth.

TABLE 2. Temperature Decorrelation Depth and Mixed Layer Depth by Region and Season

| | Winter | Spring | Summer | Fall |
|---|---|---|---|---|
| *Central California* | | | | |
| Coastal | | | | |
| Decorrelation depth | 32-- | 51+ | 21+++ | 35+++ |
| Mixed layer depth | 41 | 26 | 14 | 19 |
| Transition | | | | |
| Decorrelation depth | 55 | 79+ | 45+++ | 35 |
| Mixed layer depth | 47 | 44 | 24 | 27 |
| Oceanic | | | | |
| Decorrelation depth | 114+ | 251 | 111++ | 107+ |
| Mixed layer depth | 59 | 65 | 30 | 33 |
| *Point Conception* | | | | |
| Coastal | | | | |
| Decorrelation depth | 27--- | 30 | 30+++ | 27++ |
| Mixed layer depth | 36 | 27 | 18 | 22 |
| Transition | | | | |
| Decorrelation depth | 130++ | 71++ | 49 | 38+ |
| Mixed layer depth | 48 | 48 | 29 | 30 |
| *Southern California* | | | | |
| Coastal | | | | |
| Decorrelation depth | 30 | 20--- | 15+ | 16 |
| Mixed layer depth | 31 | 24 | 14 | 16 |
| Transition | | | | |
| Decorrelation depth | 64 | 67 | 44+++ | 32 |
| Mixed layer depth | 53 | 55 | 34 | 31 |
| Oceanic | | | | |
| Decorrelation depth | 158+++ | 74 | 34- | 38 |
| Mixed layer depth | 70 | 73 | 46 | 41 |
| *Border* | | | | |
| Coastal | | | | |
| Decorrelation depth | 32 | 14--- | 11 | 16 |
| Mixed layer depth | 30 | 17 | 11 | 15 |
| Transition | | | | |
| Decorrelation depth | 46 | 44 | 18--- | 23--- |
| Mixed layer depth | 48 | 47 | 25 | 29 |
| *Northern Baja California* | | | | |
| Coastal | | | | |
| Decorrelation depth | 47++ | 46+++ | 34+++ | 30+++ |
| Mixed layer depth | 35 | 26 | 15 | 18 |
| Transition | | | | |
| Decorrelation depth | 55 | 45-- | 24--- | 32 |
| Mixed layer depth | 56 | 58 | 31 | 31 |
| Oceanic | | | | |
| Decorrelation depth | 54--- | 75 | 31 | 37 |
| Mixed layer depth | 66 | 68 | 36 | 36 |
| *Punta Eugenia* | | | | |
| Coastal | | | | |
| Decorrelation depth | 46+++ | 41+++ | 18+++ | 29+++ |
| Mixed layer depth | 33 | 24 | 13 | 16 |
| Transition | | | | |
| Decorrelation depth | 44-- | 72++ | 25+ | 24 |
| Mixed layer depth | 49 | 49 | 22 | 25 |

Symbols denote $P(r^2=0.50$ at mixed layer depth); +, $P<0.05$; ++, $P<0.01$; +++, $P<0.001$. Plus signs mean that decorrelation depth is deeper than mixed layer depth; minus signs mean that decorrelation depth is more shallow than mixed layer depth.

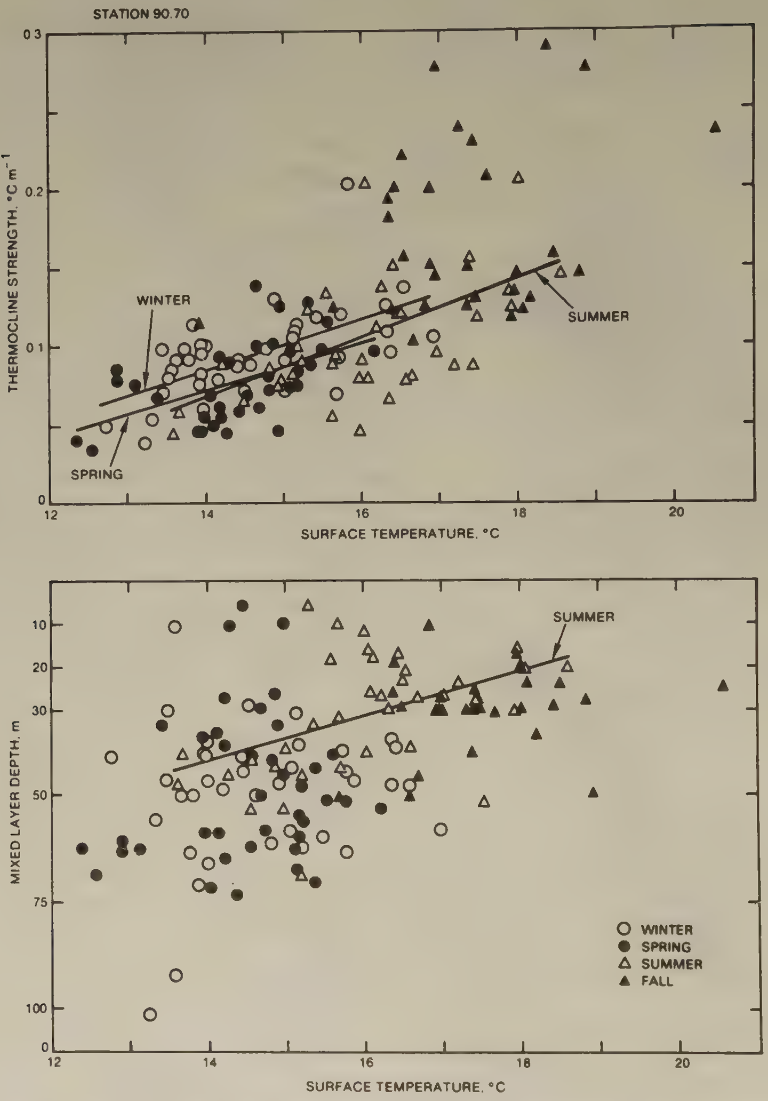

Fig. 8. (Top) mixed layer depth versus surface temperature and (bottom) thermocline strength versus surface temperature at CalCOFI station 90.70. Significant seasonal regression lines are indicated.

Southern California Bight. The flow of the California Undercurrent in these regions is coherent with the surface Inshore Countercurrent, but properties like temperature may be uncorrelated because the source waters of these currents are different (warm, salty equatorial Pacific water and cold, low-salinity subarctic Pacific water, respectively, [*Lynn and Simpson,* 1987]). The most problematic aspect of correlation minima at intermediate depths is the increase in correlation with the surface at greater depths. A single realization of such a profile might be caused by an intrusion of a different water type at the intermediate depth, but long-term mean profiles of that shape are more difficult to explain.

Correlation minima also occur year-round at 125 m in the northern Baja California oceanic region. An offshore, secondary peak in California Current flow occurs in the upper 100–150 m in this region [*Lynn and Simpson,* 1987]. Finally, correlation minima occasionally occur at 50–125 m in transition regions south of Point Conception: southern California and border in fall, northern Baja California in summer and fall, and Punta Eugenia in winter. The core of the California Current is found in these regions, but flow and distributions of properties in the surface layer are modified by mesoscale eddies [*Lynn and Simpson,* 1987]. Three-layer eddies, such as the one observed by *Simpson et al.* [1984], may be responsible for the shape of these correlation profiles.

## 5. CONCLUSIONS

Satellite imagery has proven its value in a wide range of applications, mostly limited to the surface layer of the ocean [cf. *Fiedler et al.*, 1984; *Felsher*, 1986]. Analysis of the CalCOFI data set demonstrates that sea surface data, as might be obtained by accurate remote sensing techniques, can provide some useful information about mesoscale structure in the surface layer above the seasonal thermocline and about the vertical structure of the water column through the thermocline.

Linear correlation analysis of the vertical coherence of mesoscale structure can only show that surface imagery provides information about thermocline fronts, subsurface eddies, or undercurrents where those features are coherent with surface layer fronts, eddies, or currents. The value of surface imagery used in this way requires prior knowledge based on surface and subsurface sampling. The California Current is a relatively well known system; great care must be taken when using remote sensing data to infer subsurface structure in less well known systems.

In the California Current, surface temperature provides some limited information about vertical thermal structure and subsurface mesoscale structure. Errors introduced into the temperature signal at the sea surface, in the atmosphere, and on board the satellite will further limit the utility of the data. In the future, measurements of sea surface winds from satellite scatterometers or ocean color from new color sensors may offer information complementary to sea surface temperature that would improve the precision of derived estimates of vertical structure parameters. Satellite sensors will be fully exploited for global, regional, and mesoscale studies of the marine environment when subsurface information can be reliably derived from satellite data.

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## REFERENCES

Bernstein, R. L., L. Breaker, and R. H. Whritner, California Current eddy formation: Ship, air, and satellite results, *Science, 195*, 353–359, 1977.

Dugan, J. P., Characteristics of surface temperature structure and subsurface mesoscale features, *Remote Sens. Environ, 9*, 109–113, 1980.

Felsher, M., Satellite remote sensing in oceanography — An introduction, *Mar. Technol. Soc. J., 20*(2), 3–4, 1986.

Fiedler, P. F., G. B. Smith, and R. M. Laurs, Fisheries applications of satellite data in the eastern North Pacific, *Mar. Fish. Rev., 46*(3), 1–13, 1984.

Flament, P., L. Armi, and L. Washburn, The evolving structure of an upwelling filament, *J. Geophys. Res., 90*, 11,765–11,778, 1985.

Koblinsky, C. J., J. J. Simpson, and T. D. Dickey, An offshore eddy in the California Current system, II, Surface manifestation, *Prog. Oceanogr., 13*, 51–69, 1984.

Legeckis, R., A survey of worldwide sea surface temperature fronts detected by environmental satellites, *J. Geophys. Res., 83*, 4501–4522, 1978.

Lynn, R. J., and J. J. Simpson, The California Current system: The seasonal variability of its physical characteristics, *J. Geophys. Res., 92*, 12,947–12,966, 1987.

Lynn, R. J., K. A. Bliss, and L. E. Eber, Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-*t*, stability, dynamic height, oxygen and oxygen saturation in the California Current, 1950–1978, *CalCOFI Atlas 30*, 513 pp., Univ. of Calif., San Diego, 1982.

Simpson, J. J., T. D. Dickey, and C. J. Koblinsky, An offshore eddy in the California Current system, I, Interior dynamics, *Prog. Oceanogr., 13*, 5–49, 1984.

Simpson, J. J., C. J. Koblinsky, J. Peláez, L. R. Haury, and D. Wiesenhahn, Temperature-plant pigment-optical relations in a recurrent offshore mesoscale eddy near Point Conception, California, *J. Geophys. Res., 91*, 12,919–12,936, 1986.

Sokal, R. R., and F. J. Rohlf, *Biometry*, 776 pp., W. H. Freeman, San Francisco, Calif., 1969.

Wyllie, J. G., Geostrophic flow of the California Current at the surface and at 200 meters, *CalCOFI Atlas 4*, 300 pp., State of Calif. Mar. Res. Comm., La Jolla, 1966.

Wyrtki, K., *Oceanographic Atlas of the International Indian Ocean Expedition*, 531 pp., U.S. Government Printing Office, Washington, D.C. 1971.

Wyrtki, K., L. Magaard, and J. Hager, Eddy energy in the oceans, *J. Geophys. Res., 81*, 2641–2646, 1976.

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# DYNAMIC RESPONSE ANALYSIS. II. EVALUATION OF DYNAMIC RESPONSE ANALYSIS IN A SIMULATED NO-HARVEST CASE

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## ABSTRACT

A new method of stock assessment, dynamic response analysis, allows a qualitative assessment of stock status relative to its level of maximum net productivity to be carried out with minimal data. This paper evaluates the performance of dynamic response analysis on a simulated population under variable conditions with uncertain data. In the no-harvest case the data consist simply of a temporal sequence of relative population sizes. Dynamic response analysis is most sensitive to the number and precision of the population estimates and least sensitive to environmental variability and the intrinsic population growth rate. Significance levels must be chosen carefully, since some combinations of parameters and error levels result in an unacceptably low proportion of correct assessments. Dynamic response analysis can be a useful stock assessment technique for the management of marine mammals, but attention must be paid to the quantity and quality of the data.

Key words: dynamic response analysis, marine mammal management, Marine Mammal Protection Act.

Dynamic response analysis is a method of stock assessment applicable to a population for which recent records of abundance estimates and harvests are available. The method was developed recently at the Southwest Fisheries Center, National Marine Fisheries Service, in response to monitoring obligations under the Marine Mammal Protection Act. It is, however, a general management technique. Dynamic response analysis determines whether a population is above or below its maximum net productivity level (MNPL). The theory behind the analysis is presented by Goodman (1988). This paper explores the amount and precision of data required for dynamic response analysis to work satisfactorily. The third paper in the series applies the analysis to several northern elephant seal populations (Boveng *et al.* 1988).

One application of dynamic response analysis utilizes an index of population abundance over time, augmented by harvest data, if any, to determine whether the population growth rate is accelerating or decelerating. A number of potential sources of error could affect the assessment. Environmental conditions may vary, for example, or there may be uncertainty in estimating population size. Before dynamic response analysis is used as a management tool, its robustness to the kinds of data likely to be found in actual practice should be evaluated. The sensitivity of dynamic response analysis to variable and uncertain data is investigated in this paper by analyzing a simulated population with known variability and measurement error.

## METHODS

The robustness of dynamic response analysis is measured by estimating, under various conditions, the probability that the analysis will give a correct assessment of population size relative to its MNPL. In particular, dynamic response analysis is applied to a depleted population recovering in the absence of harvest. The density-dependent dynamics follow the logistic model. For the no-harvest case, the data consist of estimates of population size (or an index of relative population size) spanning some number of years. The following questions are posed: (1) How many population estimates (censuses) will be required for dynamic response analysis to work reasonably well? (2) How precise must the population estimates be? (3) How sensitive is the method to the growth rate of the population? (4) How sensitive is the method to environmental variation? (5) How powerful is the method when a significance test is applied? While some details of the results will depend on the specific properties of the logistic model, there are general answers to these questions that will apply, regardless of details, for a wide range of forms of density dependence.

To simulate errors in estimating population size, the sequence of population estimates is chosen from Gaussian distributions whose means are the actual population size (following deterministic logistic growth) and whose variances, expressed as the coefficient of variation, are set as an input parameter. To simulate environmental variability, the carrying capacity parameter $K$ in the logistic model is chosen, at each time step, from a Gaussian distribution whose variance is set as an input parameter. Since, in the logistic model, the population's present growth rate is determined by the difference between present population size and the maximal population size at carrying capacity, this variation in carrying capacity will cause the observed growth rate to fluctuate. The mean carrying capacity is fixed at unity.

Given a sequence of population estimates with some variability, the status of the population relative to the logistic MNPL of 0.5 may be determined by fitting a second-degree polynomial to the population estimates and examining the sign of the second-degree regression coefficient (Goodman 1988). A negative coefficient indicates that the growth rate is decreasing, and hence that the population is above the MNPL, while a positive coefficient indicates the opposite. Whether the assessment is correct or not depends on whether the midpoint of the deterministic growth sequence is above or below the MNPL. Even in a deterministic system without measurement error, ambiguity about the assessment of a sequence of population estimates arises when the sequence includes the MNPL. In this paper the midpoint of the sequence has been chosen as a reference point; this ensures that a population trajectory including the MNPL will be assessed in conformity with the majority of the population estimates it contains. Each simulation was repeated 1,000 times, and the proportion of correct assessments was taken as an estimate of the probability that dynamic response analysis would be correct at that population level. In this implementation of dynamic response analysis, therefore, no statistical test is performed, but the proportion of correct assessments is analogous to the power of the technique—that is, its ability to reject a false case.

The decision strategy outlined above, which considers the direction of the population growth curvature only, is the simplest application of dynamic response analysis. Because it is easy to understand and apply, this decision strategy has been employed in the following simulations to assess relative sensitivity. In actual practice, however, dynamic response analysis is unlikely to be used in such a simplistic manner. Other kinds of information will usually be available and, if so, can be used to increase the power of the analysis considerably. For example, rough estimates of past abundance can help interpret current estimates, even though past estimates are not sufficiently quantitative to be used as part of a dynamic response analysis.

As one illustration of a more realistic application of dynamic response analysis, the results of a second series of simulations with a more refined decision process are presented. In these simulations it is assumed that something is known of the precision of the population estimates, and both linear and polynomial regressions are computed for each temporal sequence of estimates. The magnitudes as well as the signs of the linear regression coefficient (the slope) and the second-degree polynomial regression coefficient (the curvature) are considered. If the slope is negative, or if it is not significantly different from zero, this is taken as evidence that the population is above the MNPL. If the slope is significantly positive, the curvature then indicates whether the population is below the MNPL (second-degree polynomial regression coefficient significantly positive), near the MNPL (coefficient not significantly different from zero), or above the MNPL (coefficient significantly negative). The null hypothesis in each case is that the regression coefficient is not significantly different from zero. In each simulation the parameter values are used to generate the true case, and we are evaluating the ability of dynamic response analysis to recognize, after evaluating the significance of the two coefficients, the true case as one of these three levels.

For the simulations reported here, the region "near the MNPL" has been defined as the range of population sizes from 0.4 to 0.6 (as a fraction of *K*). Within this range, if dynamic response analysis determines that the population is either below or near the MNPL, the assessment is tallied as correct. Above a population size of 0.6, only determinations of above MNPL are counted as correct. This classification represents a biologically conservative management approach in which the standards for deciding that the population is above the MNPL (and harvesting, therefore, may be permitted) are more stringent than

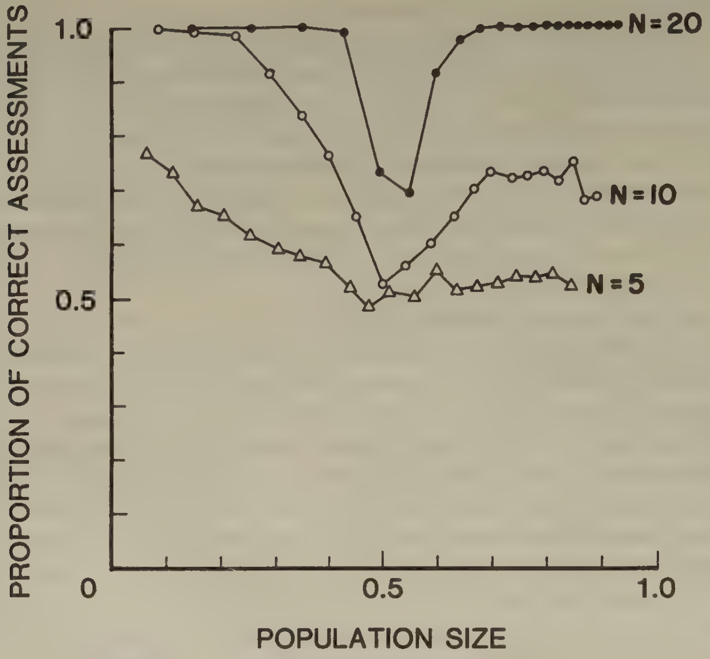

*Figure 1.* The proportion of correct assessments by dynamic response analysis as a function of population size and $N$, the number of population estimates used in each assessment. Values of other parameters are the coefficient of variation of the population estimates (CV) = 0.05, the logistic parameter of maximum intrinsic population growth rate ($r$) = 0.15, and the standard deviation of the variation in carrying capacity ($\sigma_K$ = 0.0).

the standards for deciding that the population is below the MNPL (and protection, therefore, is called for). Other strategies are of course possible.

## RESULTS

The results of the simulations are presented in Figures 1–7. The probability of a correct assessment by dynamic response analysis is plotted as a function of population size. Each figure typically shows that dynamic response analysis does well at low population levels, but shows a decline near the MNPL (0.5) to about 0.5. This is not surprising. At the MNPL the second derivative of the population growth curve is changing in sign, so a sequence of population estimates centered on this point is about equally likely to show positive as negative curvature. The goal is to confine this decline in assessment accuracy to as narrow a range of population sizes as possible.

Figure 1 presents three curves which show the effect of different numbers of data points. The parameter $N$ represents the number of population estimates available. The lowest curve, for $N = 5$, shows that a sequence of five population estimates is not sufficient, at a value of $r = 0.15$, for dynamic response analysis

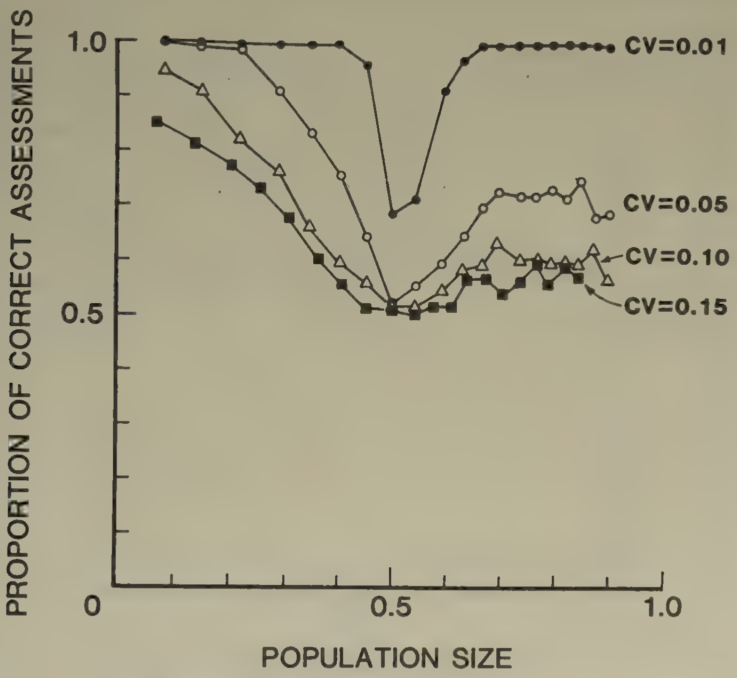

*Figure 2.* The proportion of correct assessments by dynamic response analysis as a function of population size and CV, the coefficient of variation of the population estimates. Values of other parameters are $N = 10$, $r = 0.15$, and $\sigma_K = 0.0$.

to work satisfactorily except at very low population levels. There is considerable improvement in the ability to detect a population's status correctly with a sequence of 10 population estimates (middle curve in Fig. 1). With 20 censuses, the technique works very well except in a narrow band near the MNPL. Thus, the analysis is relatively sensitive to the length of the time-series of population estimates.

Figure 2 presents four curves which contrast the effects of the precision of the population estimates. Precision is measured by the coefficient of variation (CV), the ratio of the standard deviation to the mean. When the coefficient of variation is very low (0.01)—that is, with highly precise population estimates—the technique is definitive except in a narrow band near the MNPL. This band rapidly expands as the coefficient of variation increases to 0.05, 0.1 and 0.15 (Fig. 2). As discussed later, even a coefficient of variation of 0.15 is considered fairly precise for many types of population estimation. Therefore, the simulations indicate relatively high sensitivity to the precision of the population estimates.

Figure 3 presents curves which show the effect of different rates of population growth. The logistic parameter $r$, which is used here to indicate population growth rate, is the maximum growth rate the species can achieve under uncrowded conditions and abundant resources. The unit of time is the interval between population estimates. In the logistic model the growth rate declines linearly with density, so that at the MNPL of 0.5 the growth rate will be $r/2$. Figure 3 shows that populations capable of more rapid growth will be analyzed

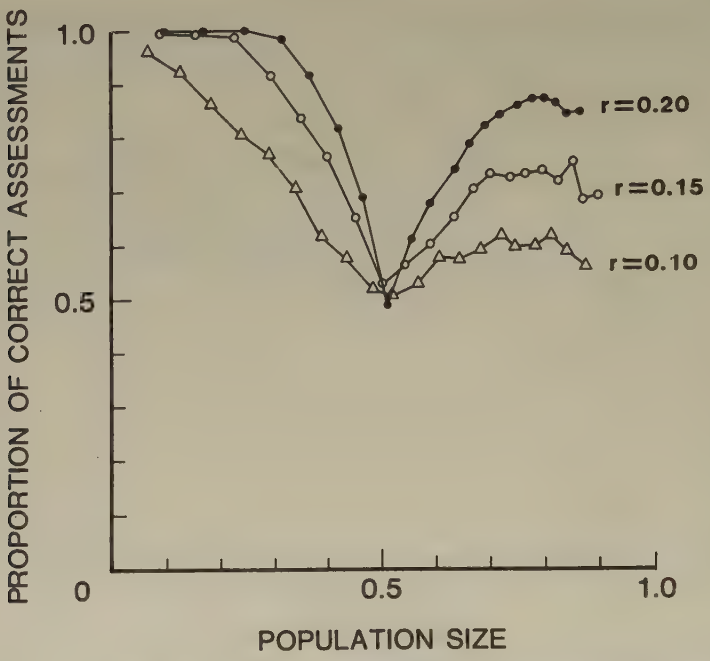

*Figure 3.* The proportion of correct assessments by dynamic response analysis as a function of population size and *r*, the logistic parameter of maximum intrinsic population growth rate. Values of other parameters are $N = 10$, CV = 0.05, and $\sigma_K = 0.0$.

correctly by dynamic response analysis more often than populations with lower growth rates.

Figure 4 shows the effect of environmental variability on dynamic response analysis. The variability is measured by the standard deviation of the carrying capacity $\sigma_K$. In these simulations it is assumed that there is no error in the estimation of population size. As the environment becomes more variable, dynamic response analysis is less effective above the MNPL, but even at the highest level of environmental variability shown here ($\sigma_K = 0.15$), the probability of a correct assessment remains high except in the vicinity of the MNPL.

In Figure 5 the stochastic effects of estimation error and environmental variability are combined. Each curve has a specified precision to the population estimates, measured by the coefficient of variation, and a specified variation in the environment, measured by the standard deviation of the carrying capacity. Three cases, ranging from small (CV = 0.05, $\sigma_K = 0.05$) to large (CV = 0.15, $\sigma_K = 0.15$) variability, are shown. As expected, the proportion of correct assessments decreases with increasing variability in both parameters.

As discussed under Methods, the simulations reported in Figures 1–5 simply use the sign of the second-degree polynomial regression coefficient as the decision statistic. Figures 6 and 7 include the results of a more refined application of dynamic response analysis, using significance tests with both linear and polynomial regressions. These simulations show how a knowledge of the precision of the population estimates can be used to increase the power of the analysis

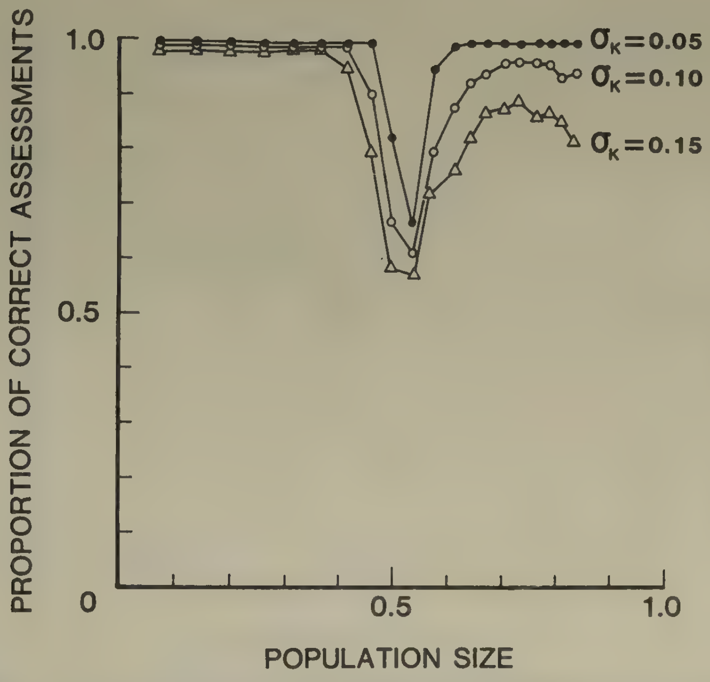

*Figure 4.* The proportion of correct assessments by dynamic response analysis as a function of population size and $\sigma_K$, the standard deviation of the variation in carrying capacity. Values of other parameters are $N = 10$, CV = 0.0, and $r = 0.15$.

greatly. They also provide more realistic estimates of the probability that dynamic response analysis will assess the population correctly.

Figure 6 compares two curves given a sequence of 10 population estimates, an intrinsic population growth rate of 0.15, and a coefficient of variation of 0.3. The lower curve with open triangles is similar to the curves presented in Figures 1–5; that is, it relies on the sign of the second-degree regression coefficient only. Because the coefficient of variation of the population estimates is relatively high (CV = 0.3), the curve remains near 0.5 over a wide range of population sizes. Under these conditions, in other words, the assessment is little better than chance. The upper curve shows the improvement possible by using significance tests on both the linear and polynomial regression coefficients. The significance ($\alpha$) levels were set at 5% for the linear regression and at 10% for the polynomial regression. With this procedure, dynamic response analysis is able to assess the status of the population correctly over a wide range of population sizes, even with relatively imprecise population estimates.

Significance levels must be chosen carefully, however, to avoid a drop in the proportion of correct assessments. Figure 7 shows a comparison among three curves, using an example when only five population estimates are available. With such a short time-series ($N = 5$), the sign of the second-degree regression coefficient alone is not very informative, even though the population estimates are precise (CV = 0.05). This is shown by the curve with open triangles in

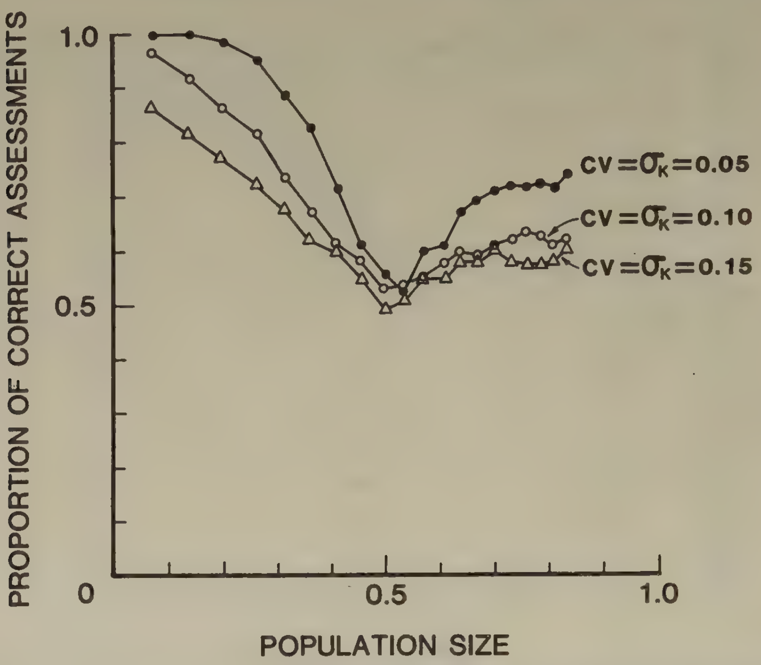

*Figure 5.* The proportion of correct assessments by dynamic response analysis as a function of population size, precision of population estimates (CV), and environmental variability ($\sigma_K$). Values of other parameters are $N = 10$ and $r = 0.15$.

Figure 7 (a similar curve is shown in Fig. 1) which is again near a proportion of 0.5 correct assessments over a wide range of population sizes. The curve with closed circles shows the performance of the more "advanced" version of dynamic response analysis, using significance levels of 5% and 10% for the linear and polynomial regressions, respectively, as in Figure 6. In this case, however, the analysis does well at low population levels, drops sharply at population sizes above 0.6, and then increases to become high again at population sizes near *K*. This effect is due to the relative strengths of the "signals" given by the linear and polynomial regression coefficients. In the range of population sizes from about 0.6 to 0.8, the slope is usually significant but curvature is not, indicating (incorrectly) that the population is near the MNPL.

When the significance test for the detection of slope is made more stringent ($\alpha = 0.01$) and the significance test for the detection of curvature more lenient ($\alpha = 0.2$), the sharp drop in the proportion of correct assessments can be avoided, as shown by the curve with open circles in Figure 7. This latter choice of significance levels leads to satisfactory performance by dynamic response analysis over a wide range of population sizes, as before, and a considerable improvement over relying on the sign of the polynomial regression coefficient alone. Further simulations have shown that the optimal choice of significance levels depends mainly on the number and precision of the population estimates. The nature of the dependence appears to be complicated and no simple rules are offered.

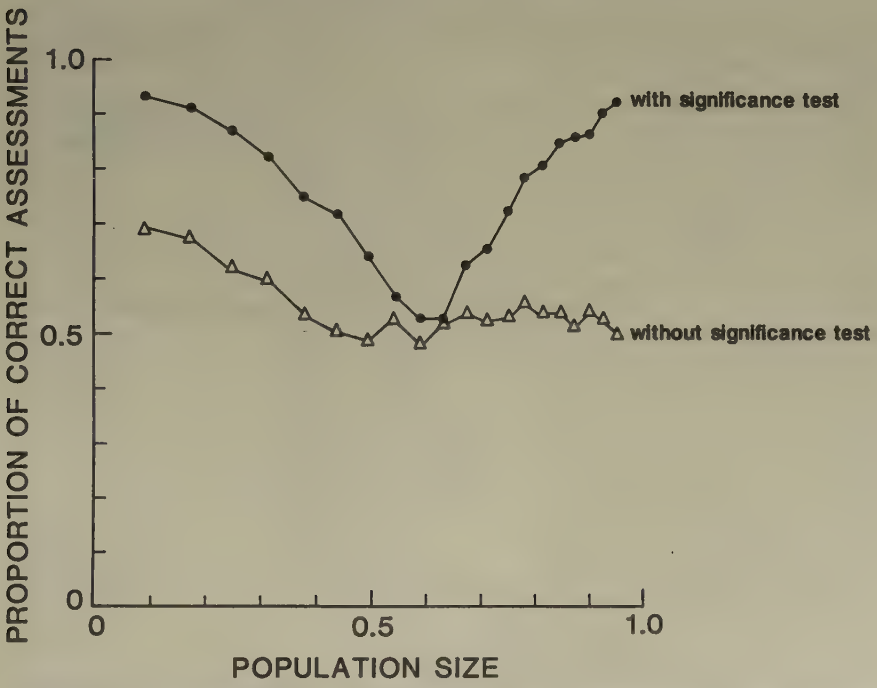

*Figure 6.* Comparison of the proportion of correct assessments by two different implementations of dynamic response analysis. Values of parameters are $N = 10$, CV = 0.3, $r = 0.15$, and $\sigma_K = 0.0$. Curve with open triangles relies on the curvature of the population growth trajectory only. Curve with closed circles uses a decision procedure which tests the significance of the slope at the 5% level and of the curvature at the 10% level.

However, given the number and precision of the population estimates, optimal significance levels can be found using simulations, as in Figures 6 and 7.

## DISCUSSION

The simulations described in this paper examine the robustness of two particular implementations of dynamic response analysis under variable conditions with uncertain data. The results presented in Figures 1–4 show that dynamic response analysis is more reliable (1) with a longer sequence of population size estimates, (2) with more precise population estimates, (3) with populations capable of higher intrinsic growth rates, and (4) with lower environmental variability. The qualitative results for these related factors agree with intuition because each either provides a stronger "signal" about population growth rate or allows that signal to be more clearly perceived.

The second set of simulations gives more quantitative estimates of the probability that dynamic response analysis will correctly determine whether a population is above or below its MNPL. Most of the parameter values in the simulations were chosen to approximate values which could be met in the actual

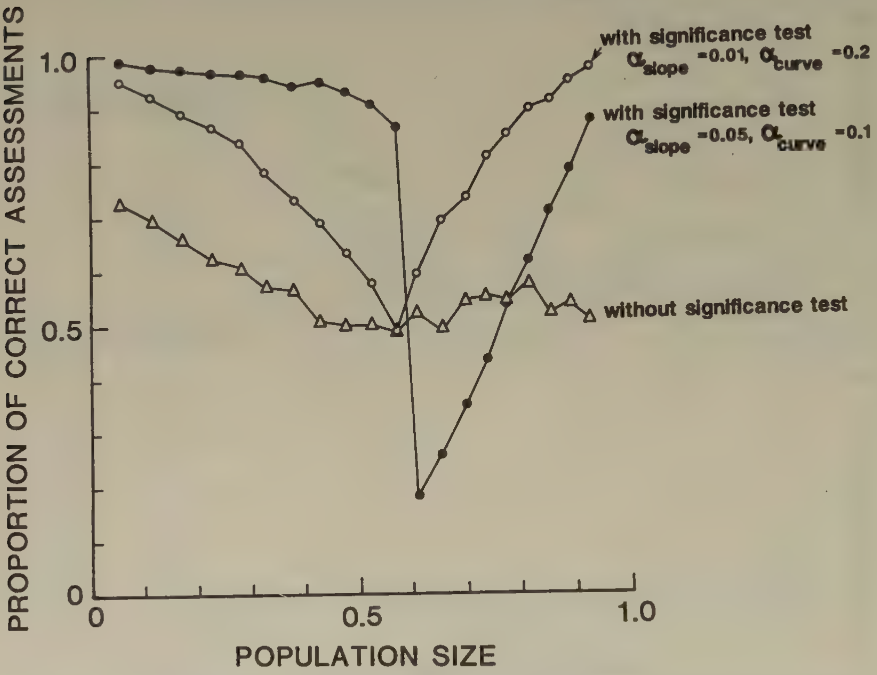

*Figure* 7. Comparison of the proportion of correct assessments by dynamic response analysis using different significance levels. Values of parameters are $N = 5$, CV = 0.05, $r = 0.15$, and $\sigma_K = 0.0$. Curve with open triangles relies on the curvature of the population growth trajectory only. Curve with closed circles uses a decision procedure which tests the significance of the slope at the 5% level and of the curvature at the 10% level. Curve with open circles uses the same decision procedure but with significance levels set at 1% for the slope and 20% for the curvature.

study of large mammals. It is clear that dynamic response analysis is capable of telling whether an unharvested population is above or below its MNPL merely from an historical sequence of abundance estimates. However, it is also clear that data used in a dynamic response analysis will have to satisfy fairly stringent conditions before much confidence can be placed in the result.

Probably the most stringent data requirement is a precise method of estimating population abundance (or an index of relative population abundance). It is hardly surprising that a method of stock assessment which relies, as dynamic response analysis does, on the differences in estimated abundance in successive time periods should be very sensitive to the precision of those abundance estimates. Figure 7 shows that, with $r = 0.15$ and as few as 5 estimates, dynamic response analysis can perform satisfactorily if the coefficient of variation is 0.05 or less. This is rather high precision. Most field studies report less precise estimates of abundance (higher coefficients of variation). Table 1 summarizes the precision of some direct counts of abundance which have been reported for large mammals. All the reported coefficients of variation fall above 0.05, although precision in the range 0.05–0.1 is not impossible to achieve under the right conditions.

*Table 1.* Precision of direct estimates of abundance for some populations of large mammals. Some of the values for the coefficient of variation (CV) are derived while others are estimated empirically.

| Species | Method | CV | Reference |
|---|---|---|---|
| Sea lion | Replicated ground counts of live pups | 0.06 | Calculated from DeLong *et al.*[a] |
| Moose | Aerial counts under excellent conditions | 0.1 | LeResche and Rausch 1974 |
| Gray whale | Derived from shore counts during migration | 0.1 | Reilly *et al.* 1983 |
| Large ungulates (6 species) | Derived from aerial quadrat counts | 0.11–0.18 | Laws *et al.* 1975 |
| Sea otter | Replicated aerial strip transects | 0.13 | Estes[b] |
| Porpoise | Derived from aerial line transects | 0.16 | Smith 1981 |
| Sperm and fin whales | Derived from catch statistics | 0.16–0.46 | Allen and Kirkwood[c] |
| White-tailed deer | Helicopter censuses | 0.2 | Beasom 1979 |
| Bottlenose dolphin | Aerial strip transects | 0.42–0.67 | Leatherwood *et al.* 1978 |
| Walrus | Aerial strip transects | 0.25–0.99 | Estes and Gilbert 1978 |

[a] DeLong, R. L., G. A. Antonelis and E. Jameyson. 1982. California sea lion pup production, premature birth, and neonatal mortality on San Miguel Island, 1969–1981. Unpublished manuscript. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115.

[b] Estes, J. A. 1982. Aerial surveys of the California sea otter population, winter 1981–82. Unpublished manuscript. Center for Marine Studies, University of California, Santa Cruz, CA 95064.

[c] Allen, K. R., and G. P. Kirkwood. 1976. Is experimental management of whale stocks practicable? Paper ACMRR/MM/SC/Cmt. 3, FAO Scientific Consultation on Marine Mammals, Bergen.

Indirect methods of abundance estimation, such as estimates derived from mark-recapture data, will usually be less precise than the direct counts shown in Table 1. Fortunately, low precision can be compensated for by a longer temporal sequence of abundance estimates. Figure 6 shows, for example, that a coefficient of variation of 0.3 can still give quite satisfactory results if there are 10 abundance estimates rather than only 5. A coefficient of variation of 0.3 is within a practical range of precision for many population studies.

It is important to recognize that the variation in abundance estimates simulated here is due, in actual practice, to a combination of many factors, including counting errors, differences among observers, variation in sighting conditions, and variation in availability. It could be estimated by a replicated series of counts under actual conditions. However, this measurement error is a minimum estimate of the variation to be expected in a temporal series of abundance estimates (Harris 1986, Gerrodette 1987). Internal population events, such as changes in behavior or age structure, as well as external changes in the environment, also contribute variability to a series of estimates. Furthermore, a time-series may have positive autocorrelation. These factors should be recognized if precision is estimated from the residuals of a regression of abundance estimates over time.

The simulations have also shown that a reasonably long temporal sequence of abundance estimates is required. As noted above, there is an inverse relationship between the required number and precision of the estimates, so that dynamic response analysis may work equally well with a short sequence of precise estimates or a long sequence of imprecise estimates. The short sequence of precise estimates is to be preferred, however, since the longer the time, the less certain we are that other factors are remaining constant. If the precision of the population index is known, the length of the time-series needed for dynamic response analysis to work satisfactorily can be computed. Boveng *et al.* (1988) explore ways of choosing the length of the time-series even when precision is not known.

Based on the range of parameters reported in these simulations, dynamic response analysis appears less sensitive to environmental variability and the rate of population growth (Figs. 3 and 4). The most variable environment simulated had a coefficient of variation of 0.15 in the carrying capacity $K$. With normally distributed variation, this means that approximately 95% of the time the carrying capacity is between 0.7 and 1.3 times its long-term mean value. Simulated values of the intrinsic population growth rate $r$, where time is scaled in units of interval between population estimates, ranged from 0.1 to 0.2. Since observed maximum population growth rates will generally be less than the theoretical maximum logistic parameter $r$, this range of values for $r$ is appropriate on an annual basis for pinnipeds (Eberhardt and Siniff 1977, Payne 1977, Eberhardt 1981, Cooper and Stewart 1983), but perhaps slightly high for most cetaceans (Kasuya 1976, Best 1981, Reilly 1984, Breiwick *et al.* 1984, Reilly and Barlow 1986).

For management purposes, a determination that the population is "near the MNPL" is, although not precise, nevertheless informative and useful. In cases of conservative management, such as mandated by the Marine Mammal Protection Act, a population in the immediate vicinity of its MNPL would be managed as if it were below the MNPL—*i.e.*, measures would be taken to protect and increase the size of the population. This conservative management policy is the reason why population densities near the MNPL have been grouped together with densities below the MNPL in this paper.

To reach an assessment that the population is near the MNPL, the significance of the slope and the curvature of the population growth trajectory were evaluated in the second set of simulations. However, when using dynamic response analysis in this way, the significance levels must be chosen carefully. As shown in Figure 7, the use of inappropriate significance levels could result in a low probability of correct assessment over a certain range of population sizes. Such a loss in power can be avoided by the appropriate choice of significance levels, given the number and precision of the population estimates, as shown by the curve with open circles in Figure 7.

The general features of the sensitivity of dynamic response analysis reported in this paper do not depend on the specific nature of the density-dependent response of the population. As emphasized by Goodman (1988), dynamic response analysis makes only a few assumptions about the density-dependent dynamics of a population, and these assumptions are almost certainly satisfied by an actual population. The simulations reported here used the logistic model as a specific example. The results therefore show a decline in power near the logistic MNPL of 0.5, but this decline is expected to occur wherever the MNPL happens to fall for a specific population. Fowler (1981) has argued that for large mammals, the MNPL occurs at a population size which may be near the carrying capacity, whereas for fish, the MNPL will be a smaller fraction of *K*. In other words, the yield curve may be skewed to the left or right. One of the strengths of dynamic response analysis is that it does not attempt to estimate the actual MNPL or the shape of the yield curve, but only to answer the qualitative question at hand: whether the population is above or below the MNPL.

Although it does not matter to dynamic response analysis whether the yield curve is symmetric or not, the "peakedness" of the curve will determine how wide the decline in power of the analysis near the MNPL will be. This is because it is the slope of the curve that dynamic response analysis is trying to estimate. If the yield curve has a sharp peak, it will be relatively easy to tell whether the population is on one side or the other. On the other hand, if the yield curve is rather flat-topped, so that the growth rate of the population changes little in response to population size, the effective MNPL is indistinct. This latter situation will reduce the accuracy of dynamic response analysis near the MNPL, but for the same reason it will make the biological consequences of this inaccuracy less important.

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I thank Daniel Goodman, Peter Boveng, Terence Jackson and reviewer no. 2 for critical comments on the manuscript. I am indebted to William Perrin and Douglas DeMaster at the La Jolla Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service, where this work was supported by a National Research Council Research Associateship.

## Literature Cited

Beasom, S. L. 1979. Precision in helicopter censusing of white-tailed deer. Journal of Wildlife Management 43:777–780.

Best, P. B. 1981. The status of right whales (*Eubalaena glacialis*) off South Africa, 1969–1979. South Africa Sea Fisheries Institute Investigational Report 123:1–44.

Boveng, P., D. P. DeMaster and B. S. Stewart. 1988. Dynamic response analysis. III. Application to four northern elephant seal colonies. Marine Mammal Science 4: 210–222.

Breiwick, J. M., L. L. Eberhardt and H. W. Braham. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries and Aquatic Sciences 41:484–496.

Cooper, C. F., and B. S. Stewart. 1983. Demography of northern elephant seals, 1911–1982. Science 219:969–971.

EBERHARDT, L. L. 1981. Population dynamics of the Pribilof fur seals. Pages 197–220 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. Wiley & Sons, New York.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.

ESTES, J. A., AND J. R. GILBERT. 1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). Journal of the Fisheries Research Board of Canada 35:1130–1140.

FOWLER, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602–610.

GERRODETTE, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

GOODMAN, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. Marine Mammal Science 4:183–195.

HARRIS, R. B. 1986. Reliability of trend lines obtained from variable counts. Journal of Wildlife Management 50:165–171.

KASUYA, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Scientific Reports of the Whales Research Institute 28:73–106.

LAWS, R. M., I. S. C. PARKER AND R. C. B. JOHNSTONE. 1975. Elephants and their habitats. Clarendon Press, Oxford.

LEATHERWOOD, S., J. R. GILBERT AND D. G. CHAPMAN. 1978. An evaluation of some techniques for aerial censuses of bottlenosed dolphins. Journal of Wildlife Management 42:239–250.

LERESCHE, R. E., AND R. A. RAUSCH. 1974. Accuracy and precision of aerial moose censusing. Journal of Wildlife Management 38:175–182.

PAYNE, M. R. 1977. Growth of a fur seal population. Philosophical Transactions of the Royal Society of London, Series B 279:67–79.

REILLY, S. B. 1984. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. Pages 389–399 *in* W. F. Perrin, R. L. Brownell, Jr. and D. P. DeMaster, eds. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission, Special Issue 6.

REILLY, S. B., AND J. BARLOW. 1986. Rates of increase in dolphin population size. Fishery Bulletin (U.S.) 84:527–533.

REILLY, S. B., D. W. RICE AND A. A. WOLMAN. 1983. Population assessment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967–80. Fishery Bulletin (U.S.) 81:267–281.

SMITH, T. D. 1981. Line-transect techniques for estimating density of porpoise schools. Journal of Wildlife Management 45:650–657.

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# Observations of Deepwater Shrimp, *Heterocarpus ensifer*, From a Submersible off the Island of Hawaii

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## Introduction

In Hawaii and other Pacific island groups there has been considerable interest in the commercial potential of deepwater caridean shrimps of the genus *Heterocarpus*. Exploratory trapping surveys have shown that deepwater shrimps are widely distributed throughout the central and western Pacific (Clarke, 1972; Struhsaker and Aasted, 1974; Wilder, 1977; Intes, 1978; Brown and King, 1979; King, 1980, 1981a, 1981b, 1982, 1984, 1986; Moffitt, 1983; Gooding, 1984; Dailey and Ralston, 1986; Ralston, 1986; Moffitt and Polovina, 1987).

The Southwest Fisheries Center's (SWFC) Honolulu Laboratory of the National Marine Fisheries Service, has conducted surveys of deepwater shrimp resources in Hawaii (Gooding, 1984) and the Mariana Islands (Ralston, 1986; Moffitt and Polovina, 1987).

Despite the recent economic failure of a large commercial endeavor that was engaged in a trap fishery for *Heterocarpus laevigatus* in Hawaii, (Schlais, 1982, 1983) the deepwater shrimp resource continues to offer promise for commercial exploitation in Hawaii and indeed throughout the southern and western Pacific islands. In the Hawaiian Islands *H. laevigatus*, which occurs most abundantly in depths of 450-700 m and *H. ensifer* which has a shallower preferred depth range of 300-600 m (Clarke, 1972; Struhsaker and Aasted, 1974; Gooding, 1984; Dailey and Ralston, 1986), have been targets of trap fisheries. However, *H. laevigatus* is generally considered to have the greater commercial potential because it is larger.

At present there is no Fishery Management Plan (FMP) for deepwater shrimps. The Western Pacific Regional Fishery Management Council (Council) has identified the *Heterocarpus* resource as one in need of further basic research for effective future management[1]. The Honolulu Laboratory is presently conducting "intensive fishing experiments" on isolated *H. laevigatus* grounds to acquire estimates of absolute and relative abundance of exploitable stocks (Ralston, 1986). For management purposes there is a need for research into population biology and stock assessment, growth rates and natural mortality, and migration patterns. Commercial catch and effort data and research survey data from surface vessels provide much of this information. Visual observations from a research submersible can give a valuable insight into areas such as general behavior and microdistribution relative to types of fishing gear and the nature of the bottom (Ralston et al., 1986). Such direct observations may be very useful in interpreting data acquired by other means and in developing more efficient gear and fishing techniques.

In February 1984, we had the opportunity to use the Hawaii Undersea Research Laboratory (HURL) submersible, *Makalii* (Fig. 1), to make observations of *H. ensifer* off the northeast coast of the Island of Hawaii. The project was confined to *H. ensifer* grounds because the maximum operational depth of the *Makalii* is less than the depth at which *H. laevigatus* occurs. The objectives of the dives were to: 1) Determine factors that might cause variation in *H. ensifer* catch rates within a string of five traps, 2) observe the behavior of shrimp in the vicinity of two different trap designs, 3) document observed distribution and abundance of shrimp relative to type of substrate, 4) set bait on the bottom as an attractant to acquire further insight into shrimp density relative to type of substrate, and 5) collect shrimp specimens, bottom sediment, and water samples for a laboratory assay of incident bacteria. A problem for the shrimp industry that has limited the marketability of *Heterocarpus* spp. has been a rapid deterioration in the meat, so-called "mushy tail." This is believed to be caused by bacteria of the genus *Vibrio*. Four species of the genus had been identified by one of the authors (Dailey) in cultures of shrimp landed from commercial traps. We hoped to determine if these bacteria are either always on the shrimp and cause no problem for the living animal, or are subsequently picked up in the upper water column, or even after the shrimp has been landed on the vessel.

Because the *Makalii* became available

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[1] Western Pacific Regional Fishery Management Council. 1984. Draft assessment of resources, existing and potential fisheries, and management needs for selected crustacean species in the Western Pacific region. Rep. on file at Western Pacific Regional Fishery Management Council, 1164 Bishop Street, Suite 1405, Honolulu, HI 96813.

for the project on very short notice, we were able to fabricate and transport only six shrimp traps to Hawaii from Oahu. Four traps were lost early in the project so we were unable to acquire any information on the catch of similar traps on a string in relation to substrate variations.

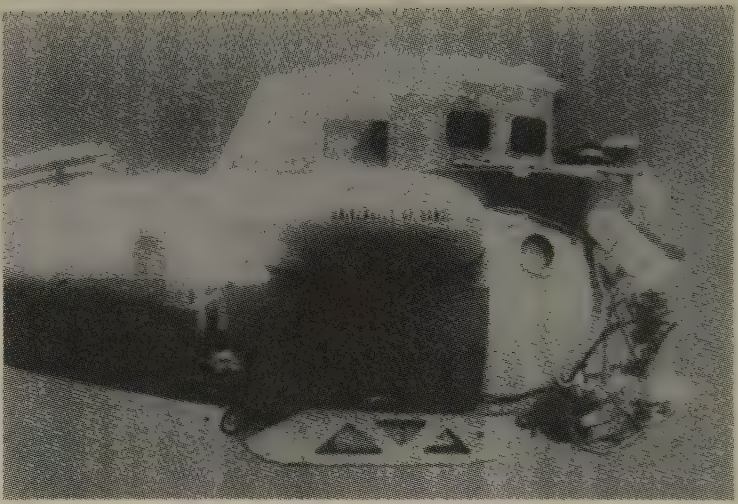

Figure 1.—The NOAA submersible, *Makalii*.

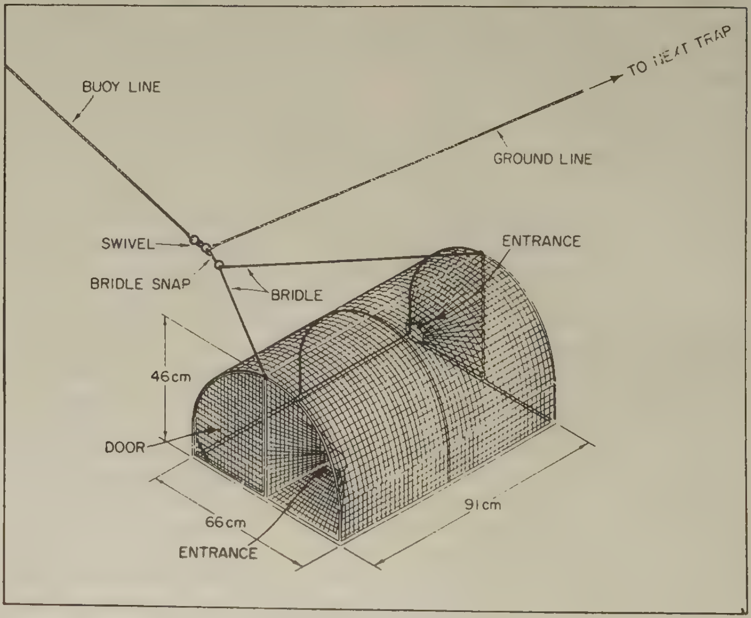

Figure 2.—Half-round shrimp trap.

## Methods

The *Makalii* is a two-man, battery-powered, one-atmosphere submersible owned and operated by HURL, University of Hawaii, and funded by the National Oceanic and Atmospheric Administration (NOAA), National Undersea Research Program (NURP). It is 4.8 m long and has a spherical capsule 1.5 m in diameter. With a pilot and one observer and up to 95 kg payload, it has an operational depth capability of about 366 m and a dive duration of 4-5 hours with emergency life support for 72 hours. Normal operating speeds range from 1 to 3 knots.

During this study, equipment that was used included: Hydraulic manipulator, two-color video cameras with monitors, recorders, and video lights, externally mounted 35 mm still camera and strobe, current and temperature meters, dictaphone tape recorder, directional antenna, and sonic pingers for site relocation. A Motorola Mini-Ranger Falcon[2] navigation system provided very precise (within 15 m) position fixes for the support vessel which tracks the submersible with an Edo Western submersible tracking system. The *Makalii* is also equipped with a Neil Brown environmental monitoring package for continuous recording of temperature, salinity, conductivity, pH, oxygen, and depth.

While on the bottom, observations were continuously video- and voice-recorded and still photographs were frequently made with the 35 mm camera and strobe.

Observations were made on two types of traps. The first was a half-rounded design with an entrance at each end (Fig. 2). This design has been used during past shrimp surveys by the SWFC Honolulu Laboratory (Gooding, 1984). The second trap was a larger pyramid-shaped design with a single entrance at the apex (Fig. 3). This was the preferred trap used in the former Hawaiian commercial fishery (Schlais, 1983). Traps were baited with Pacific mackerel, *Scomber japonicus*, and were set from the submersible support vessel. Attached sonic pingers en-

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[2] Mention of trade names or commercial firms does not imply endorsement by the authors or the National Marine Fisheries Service, NOAA.

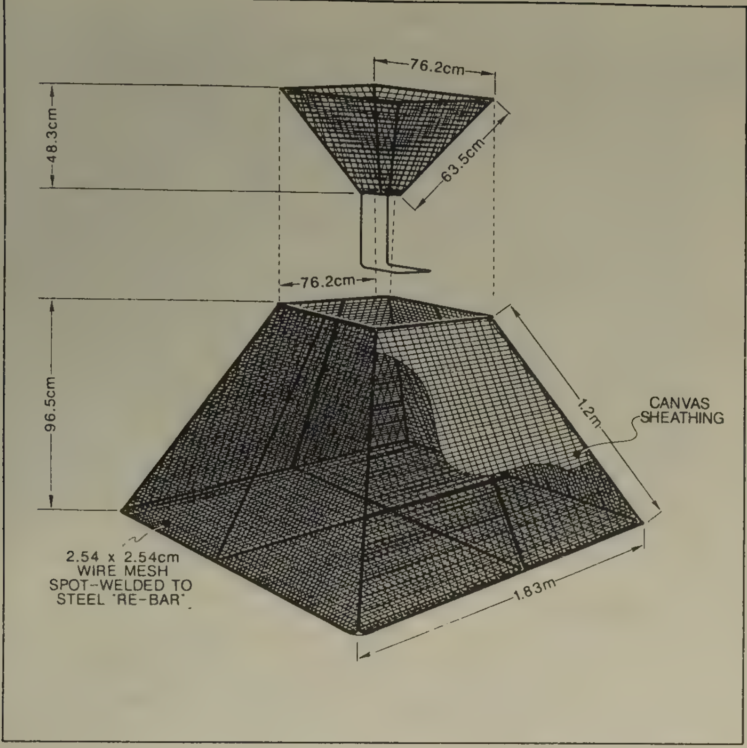

Figure 3.—Pyramid shrimp trap.

abled the submersible to locate them when it reached the bottom. Submersible observations were made on trap sets shortly after setting (1.5-5 hours) or about 24 hours after setting. The traps were retrieved after either 24 or 48 hours on the bottom. After removal from the traps the catches were held in crushed ice until later processing at dockside. Individual shrimps were not weighed. Mean individual weights were derived by dividing total weight of catch by number of shrimp.

The density of shrimp in an area was estimated by monitoring the number of shrimp aggregating to a can of tuna with numerous small punctures on all its surfaces during 10-minute intervals. The cans were sealed in plastic bags and carried in the submersible's sample storage basket. They were placed on the sea floor and the plastic bag torn away with the manipulator.

For the bacteriological tests, individual *H. ensifer* were collected from the bottom with the submersible suction collector. A bottom sediment sample was collected from the area in which shrimp were located and a sample of water close to the bottom was collected in a modified Van Dorn bottle. In the laboratory 0.1 ml of raw inoculant from each of the samples was plated on TCBS to determine total *Vibrio* and on marine agar to determine total bacteria.

The submersible observations were conducted on the Mauna Kea ledge about 12 n.mi. northeast of Hilo harbor. This general area was recommended by Edith Chave of HURL who had seen numerous *H. ensifer* there on an earlier *Makalii* dive.

## Results and Discussion

Figure 4 shows the location of the dive sites. Depths ranged from 345 to 380 m, and bottom temperature was 7°-8°C. Within these narrow ranges, temperature and depth were not correlated with either the apparent abundance of *H. ensifer* as observed from the submersible or the size of trap catches. Bottom currents were 0.2-0.3 knot (10-17 cm/second). The dives showed that for the most part the bottom was a flat basalt plain largely consisting of a shallow layer of brownish silty sand overlying volcanic lava flows. Occasionally the nearly flat relief was interspersed with small areas of low lava outcrops covered with limestone cement rising to about 20 cm above the sand. Although there was considerable amount of sediment and apparent turbidity in the upper and midwater column, water clarity at the bottom was very good except when the fine silt was disturbed by the submersible.

## Trap Observations

Five dives (*Makalii* dive No. 216-220), totaling 16.75 hours of bottom observation time, were made during 5-13 February 1984. Table 1 summarizes the schedule of dive and trapping operations. Prior to the arrival of the traps from Honolulu, on dive No. 216 we conducted a preliminary survey to determine a suitable area for subsequent trap sets and observational dives. The area surveyed on dive No. 216 consisted almost entirely of silty sand overlying a hard flat substrate. There was a high incidence of *H. ensifer* widely distributed throughout the region traversed by the *Makalii*. Shrimp densities were estimated at up to 1 per m$^3$ in some areas. Subsequent operations were conducted in the same general vicinity.

During the following four dives (217-220) we made observations on *H. ensifer* in relation to varying combinations of trap configuration, trap soak time, and bottom type.

1) Dive 217. A string of five half-round traps, spaced 16 m apart. All of the traps in the string landed upright in a depth of 347 m. They were clustered closely together on flat rubbly substrate interspersed with low outcrops. During

the observation period the traps had been on the bottom for from 1.5 to 4 hours. Only a few scattered *H. ensifer* were seen in the vicinity of the traps and the largest catch in any one trap appeared to be about four shrimp. A survey in the vicinity of the site showed the traps had landed on contiguously rocky rubbly ground apparently devoid of silty sand substrate in the vicinity. *Heterocarpus ensifer* were not seen on the rocky ground but unidentified striped shrimp were visible in small caves in the substrate. These probably were *Plesionika longirostris* which were subsequently identified on dive 219. During retrieval of the traps the following day, the groundline broke and four of the traps in the string were lost. The recovered trap contained 69 *H. ensifer* (not weighed).

2) Dive 218. A single pyramid trap which landed upright on sandy bottom at a depth of 349 m. No rocky areas were seen in the vicinity. The first observations were made about 24 hours after the trap had been set. The trap contained a large number of *H. ensifer* with many shrimp climbing up the sides, and in the funnel entrance. Many others were on the bottom surrounding the trap. The average size of the shrimp seemed so large that at first the observers thought that despite the relatively shallow depth, some of them were *H. laevigatus*. The trap was hauled the following morning after a soak-time of about 48 hours. It contained 914 *H. ensifer* weighing 16.8 kg with a mean individual weight of 18.4 g. No *H. laevigatus* were found in the catch.

3) Dive 219. A pyramid trap and a half-round trap spaced 15 m apart were deployed together. Both traps landed upright on very fine silty sand overlying a hard substrate. They were about 10 m apart at a depth of 347 m. The traps had been set the previous morning so they had been on the bottom for about 24 hours when observations began. Both traps were filled with shrimp. *Heterocarpus ensifer* were walking over the half-round trap and on the sides of the pyramid trap (Fig. 5). The surrounding sandy bottom was covered with *H. ensifer*. As had been observed during the previous trap set, the average size of the *H. ensifer* was uniformly large with very few small individuals in or around the traps. Shrimp

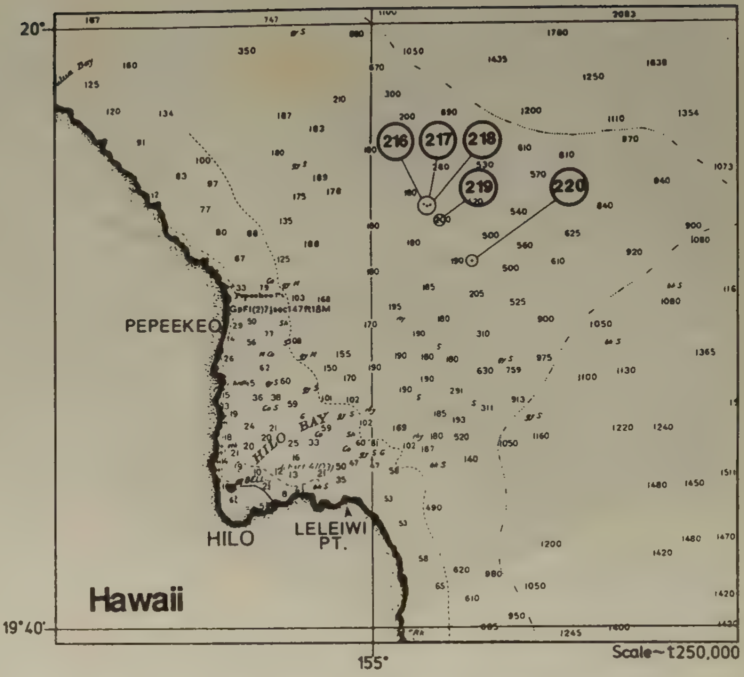

Figure 4.—Dive sites off the Island of Hawaii (soundings are shown in fathoms).

**Table 1.—Trapping observations of *Heterocarpus ensifer* during *Makalii* dives off Hawaii.**

| Observation | Dive number | | | | |
|---|---|---|---|---|---|
| | 216 | 217 | 218 | 219 | 220 |
| Depth of traps (m) | 375-385[1] | 347 | 349 | 347 | 347 |
| Bottom type | Silty sand over hard substrate | Lava rubble and low outcroppings | Silty sand over hard substrate | Silty sand over hard substrate | Silty sand over hard substrate |
| Trap soak time when observed (h) | No traps set | 1.5-4 | 24-27 | 24-27 | 1.5-4 |
| Trap soak time when hauled (h) | | 26 | 48 | 48 | 21 |
| Abundance of *H. ensifer* observed in the area | High | Low | High | High | High |
| Abundance of *H. ensifer* observed in pyramid trap | | | High | High | High |
| Abundance of *H ensifer* observed in half-round trap | | Very few | | High | High |
| No. of *H. ensifer* landed in pyramid trap | | | 914 | 1,497 | 1,676 |
| No. of *H. ensifer* landed in half-round trap | | 69 | | 1,016 | 1,110 |

[1] Range of depths observed during the dive.

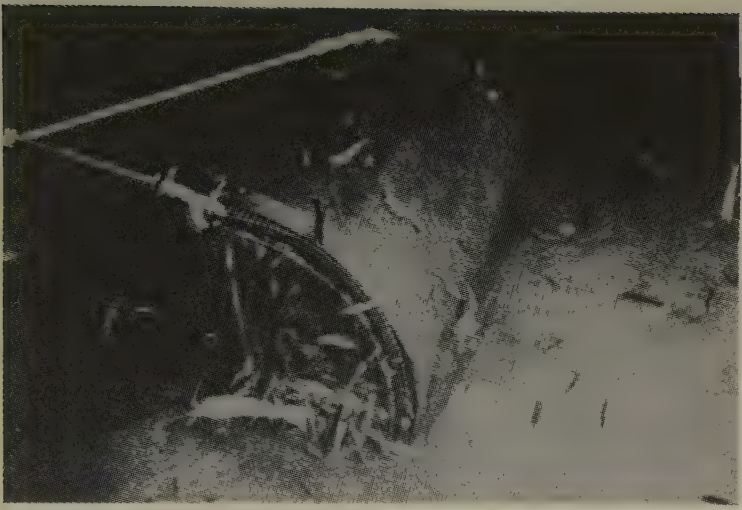

Figure 5.—Half-round trap on the bottom in a depth of 347 m; dive 219.

were frequently seen both entering and exiting the half-round trap. When they entered the conical entrance, which on this type of trap was at ground level, they usually climbed in. However, they also were observed swimming in and out. Although shrimp sometimes swam to heights approaching 2 m above the bottom, none was observed swimming into the apical entrance of the pyramid trap. They were observed in various stages of climbing up the sides of the trap towards the entrance, and into the entrance. No shrimp were observed exiting the pyramid trap. A survey of the bottom in the vicinity around the traps showed it consisted mostly of silty sand. The exception to the otherwise flat sandy topography was a small area of lava outcrops about 30 m from the trap site. There solitary striped shrimp, *P. longirostris*, were in holes and cracks in the hard substrate. The traps were hauled the following morning after being in the water for about 48 hours. The pyramid trap caught 1,497 *H. ensifer* weighing 28 kg. The half-round trap caught 1,016 *H. ensifer*, weighing 19 kg, and 7 *P. longirostris*. The mean individual weight of *H. ensifer* taken in each trap was 18.7 g.

4) Dive 220. A pyramid trap and a half-round trap spaced 15 m apart. Both traps landed on typical silty sand ground about 10 m apart in a depth of 347 m. The half-round trap was upright but the pyramid trap was on its side. The *Makalii* reached the traps about 1.5 hours after they had been set earlier that morning. The surrounding area was already covered with *H. ensifer* and shrimp were crawling over both the traps. Despite a soak time of less than 2 hours they both appeared to contain more shrimp than we had thus far seen. As on the previous dive, shrimp were both entering and exiting the half-round trap. Unfortunately, because of the danger of becoming fouled in the groundline, we were unable to get into a position to observe the entrance of the pyramid trap which in its overturned position lay close to the bottom.

During the 2.5-hour period between the first and last observations of the half-round trap there did not seem to be a noticeable increase in *H. ensifer* around or inside the trap. When it was hauled 21 hours later, the catch, although substantial, did not appear to be much different from what we had observed from the submersible. The pyramid trap caught 1,676 *H. ensifer* weighing 32 kg and the half-round trap caught 1,110 *H. ensifer* weighing 21 kg. The mean individual weights of *H. ensifer* were 19.1 g in the pyramid trap and 18.9 g in the half-round trap.

These observations showed that *H. ensifer* are attracted very rapidly to baited traps, and that a large percentage of the animals within olfactory range (depending on current conditions) may enter a trap within 2-3 hours of setting. Both traps with top entrances and those with entrances close to the substrate are efficient in allowing *H. ensifer* to enter. However, if the shrimps are satiated or the bait depleted, they apparently can more easily exit a trap with a horizontally oriented entrance near the bottom than one with a vertical top entrance. Thus small traps with bottom entrances may be more suitable for relatively short soak periods. For instance, an early morning set, and haul before noon. For longer soaks (overnight) a taller trap with a top entrance may hold the catch more efficiently.

King (1981) cited data which suggests that *H. ensifer* and *H. laevigatus* only enter traps during night. In surveys by the SWFC Honolulu Laboratory, good catches of *H. laevigatus* were made during daylight sets[3]. From deepwater photo sequences of baited traps made off Palau, Saunders (1984) found that the upper range of *H. ensifer* appeared to be strongly influenced by daily photic fluctuations. They were abundant in night sequences at 150-250 m depths, but were not recorded in daylight sequences shallower than 274 m. However, at greater depths there appeared to be no differences in either activity or numbers of individuals in day versus night photo sequence. Our trap sets were all well below 274 m. It is also likely that photic penetration is relatively limited off the east coast of Hawaii, which is subjected to considerable natural runoff as well as sugar factory effluent compared with Palauan waters. This study showed conclusively that, during peak daylight hours at the depths observed, *H. ensifer* are active feeders and will readily enter traps.

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[3] Honolulu Laboratory, Southwest Fisheries Center, 2570 Dole St., Honolulu, HI 96822-2396. Unpubl. data.

However, we are not aware of any investigation which has rigorously compared the relative merits of day and night trapping for *Heterocarpus* spp. The shrimp catches in both trap types were *H. ensifer* with the exception of the seven *P. longirostris* caught in the half-round trap observed on dive 219. No *H. laevigatus* were found in any of the catches.

We were impressed by the uniformly large size of *H. ensifer* viewed from the submersible and caught in the traps. The mean individual weights of *H. ensifer* from the two types of traps were virtually identical, at about 18.8 g. This was quite large when compared with a mean weight of 12 g for *H. ensifer* taken during trapping surveys in the NWHI (Gooding, 1984), and a maximum weight for *H. ensifer* of about 16 g reported by Struhsaker and Aasted (1974). Some studies have indicated that large *H. ensifer* occur within the depth range of maximum abundance, with smaller animals occurring both shallower and deeper (Clarke, 1972; Struhsaker and Aasted, 1974; King, 1981a). However, Moffitt and Polovina (1987) found no significant change in the size of *H. ensifer* with depth. Our observations were made at the shallow end of the range of maximum abundance for *H. ensifer* found by Gooding (1984). The submersible surveys revealed virtually no small individuals in the vicinity of the traps or the surrounding area. Thus we speculate that smaller size classes were occupying other habitats. The shrimp were not methodically sexed but inspections of the catches showed the presence of both sexes with a high incidence of berried females.

On *H. laevigatus* surveys in the Mariana Islands, Ralston (1986) found that pyramid traps outperformed half-round traps by a ratio of nearly 6:1. In this study, for the two sets (dive 219 and 220), when pyramid and half-round traps lay adjacent to one another on the same type of ground, the pyramid traps caught only 1.5 times (60 kg) the catch of the half-round traps (40 kg).

On dive 220 the pyramid trap that was lying on its side fished equally well relative to the attached half-round trap as did the upright pyramid observed on dive 219.

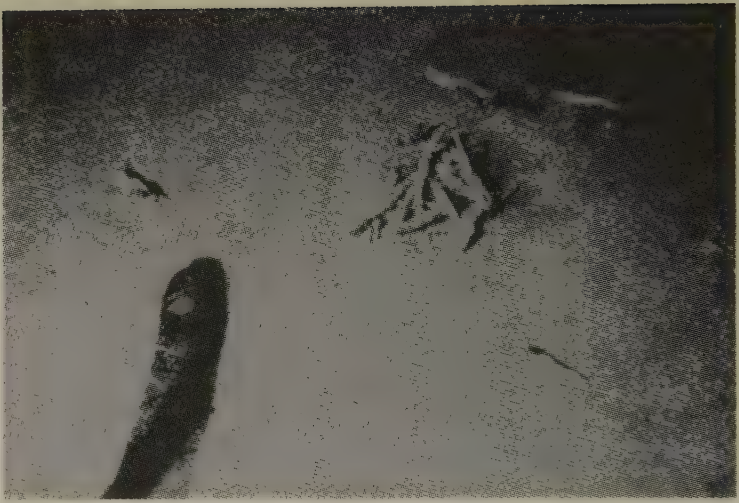

Figure 6.—*Heterocarpus ensifer* aggregated around tuna can in a depth of 347 m; dive 220.

Table 2.—Rate of *Heterocarpus ensifer* aggregation to a punctured tuna can as the number of animals observed over a 10-minute period.

| Elapsed time (min.) | Rocky outcropped bottom | | | Sandy rubble bottom | Silty sand bottom | | |
|---|---|---|---|---|---|---|---|
| | Dive 219 Test 1 | Dive 219 Test 2 | Dive 220 Test 1 | Dive 219 Test 3 | Dive 219 Test 4 | Dive 220 Test 2 | Dive 220 Test 3 |
| 1 | 1 | 0 | 0 | 1 | 2 | 2 | 7 |
| 2 | 1 | 0 | 0 | 1 | 5 | 8 | 14 |
| 3 | 1 | 0 | 0 | 1 | 9 | 13 | 20+ |
| 4 | 1 | 0 | 0 | 1 | 12 | 20 | 30+ |
| 5 | 1 | 0 | 0 | 2 | 20+ | 30+ | |
| 6 | 1 | 1 | 0 | 2 | 30+ | | |
| 7 | 1 | 1 | 0 | 2 | | | |
| 8 | 1 | 1 | 0 | 2 | | | |
| 9 | 1 | 1 | 0 | 2 | | | |
| 10 | 1 | 1 | 0 | 2 | | | |

## Tuna Can Observations

Punctured tuna cans (Fig. 6) were deployed on three substrate types: Silty sand, rocky outcroppings, and sandy rubble. Table 2 lists the number of *H. ensifer* which aggregated to the bait in each test during 10 minutes of observation. The *H. ensifer* were apparently following the odor gradient and invariably approached the can from the down-current direction. On one rocky ground test the can was placed about 2 m directly up-current of an outcropping in which we could see several *P. longirostris*; however, none of them left their holes to approach the can. On the sandy ground there was initially a rapid increase in the aggregation rate of *H. ensifer* with time which appeared to start leveling off after about 7-8 minutes. We were unable to make counts beyond about 30 animals. These crude tests clearly indicate a much higher density of *H. ensifer* on the sandy silt substrate than on the two others.

## Other Behavior

*Heterocarpus ensifer* apparently were neither attracted, repelled, nor affected in any way by the lights from the submersible. When, after a period of total darkness, the flood lights were turned on to large aggregations of *H. ensifer* gathered around traps, we were unable to discern any changes in their behavior. On dive 220 we had the opportunity for just a few seconds to observe *H. ensifer* in something approaching an undisturbed natural state. As the *Makalii*, following its descent from the surface, approached to within about 3 m of the flat sandy bottom, we were able to see *H. ensifer* all over the sandy surface out to the limits of visibility. They were solitarily distributed, about 1 per $m^2$. As the submersible settled on the bottom, some of the shrimp which were within about 1-2 m from the *Makalii* swam vertically to as high as about 2 m from the bottom. More distant shrimps, although suddenly subjected to greatly increased light, remained undisturbed. Our impression was that the disturbed *H. ensifer* were reacting to the sudden physical presence of the submersible in their midst rather than to the light.

We did not see any burrowing in the sand by *H. ensifer* on this occasion or during other observations. This supports aquaria observations which indicated that *Heterocarpus* sp. did not burrow in the substrate (King, 1986).

It is well known from the condition of shrimp in trap catches that *Heterocarpus* are cannibalistic. We did not usually observe any overt aggressive behavior amongst shrimp under the various conditions of our study. However, in two instances it was shown vividly that an *H. ensifer* that finds itself at a disadvantage to its fellows quickly becomes fair game. When the tails of animals within a trap protruded through the mesh, shrimp on the outside would start feeding on the tail, and on one occasion during observations of shrimp attracted to a tuna can, an *H. ensifer* which was injured by the submersible's manipulating arm was immediately attacked by other shrimp in the area.

## Bottom Habitat

Our observations from the *Makalii*, the subsequent trap catches, and the tuna can aggregation tests showed that of the two distinct types of substrate we encountered on Mauna Kea ledge, i.e., low profile outcropping and silty sand overlying flat substrate, the preferred type of ground for *H. ensifer* was clearly the latter. Of the six traps we recovered, the two half-round traps that landed on flat sand had a mean catch rate of 20 kg per trap whereas the half-round trap observed on rocky ground caught only 69 *H. ensifer* (probably about 1.2 kg). The three pyramid traps, all of which were on sand, had a mean catch rate of 25.6 kg per trap. Conversely, with the exception of a single *P. longirostris* observed on the bottom in front of the half-round trap on dive 219, we did not see any other of this species on sandy ground. Seven *P. longirostris* were caught in the trap which was lying about 30 m from an area of exposed hard substrate on which *P. longirostris* were seen under ledges and in small holes. No *P. longirostris* were caught in the pyramid trap on the same string. However, the half-round trap on dive 217 that lay on rocky ground where we had seen *P. longirostris*, did not catch any *P. longirostris*. Unfortunately, the other four traps on the same string were lost.

## Bacterial Tests

The results of the bacteriological culture assays (Table 3) indicate that *Vibrio alginolyticus* and another *Vibrio* sp. found commonly in and on both *H. ensifer* and *H. laevigatus* are apparently not acquired in the trap during hauling or after the shrimp are landed on the vessel.

**Table 3.—Results of bacteriological tests to determine the distribution of *Vibrio* sp.**

| Item | TCBS | Marine agar |
|---|---|---|
| Shrimp | 4+<br>*Vibrio alginolyticus* and one other *Vibrio* sp. (not identified) | 4+ |
| Bottom sediment | 2+<br>One *Vibrio* sp. found. The same as the unidentified species from the shrimp | 4+ |
| Water column | 0<br>No *Vibrio* sp. recovered | 4+ |

1+ = 100 colonies/ml
2+ = 100-500 colonies/ml
3+ = 500-2,000 colonies/ml
4+ = 2,000 colonies/ml

The indication of a 4+ growth on the *H. ensifer* compared with a 2+ growth in the surrounding bottom material implies that the shrimp are likely a primary substrate for the *Vibrio*. A 4+ on the marine agar indicates other bacteria, primarily *Pseudomonas* spp. are ubiquitous on the bottom as well as in the water column.

*Vibrio alginolyticus*, *V. parahaemolyticus*, and *Vibrio* sp. have also been found commonly on marine mammals inhabiting the upper water column (Dailey, 1985). This would tend to verify that animals rather than the water column or bottom serve as the primary substrate for these microorganisms.

## Conclusions

Because of various logistic factors the observations and tests conducted during these dives were somewhat limited in scope and sophistication. Nevertheless, the results show that valuable insights into trap siting and trap design relative to deepwater shrimp ecology and behavior and also more general aspects of the biology of shrimp can be acquired using a research submersible. This type of information can complement and supplement data collected by more conventional methods.

The HURL has recently acquired the *Pisces V*, a three-man, one-atmosphere submersible that can reach depths of 2,000 m. Planned SWFC Honolulu Laboratory studies on *H. laevigatus* from the *Pisces V* will provide information about this potentially more valuable species which, we hope, will contribute to the development and management of deepwater shrimp fisheries in Hawaii and other Pacific island areas.

## Acknowledgment

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## Literature Cited

Brown, I. W., and M. G. King. 1979. Deepwater shrimp trapping project. Report on Phase I. Minist. Agric. Fish., Fish. Div. Tech. Rep. 1, Fiji, 20 p.

Clarke, T. A. 1972. Exploration for deep benthic fish and crustacean resources in Hawaii. Univ. Hawaii, Hawaii Inst. Mar. Biol., Honolulu, Tech. Rep. 29, 18 p.

Dailey, M. D. 1985. Diseases of marine mammalia: Cetacea. *In* O. Kinne (editor), Diseases of marine animals, p. 805-846. Biol. Anstalt Helgol. Hamburg. 14(2), Chapter 7.

________ and S. Ralston. 1986. Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp, *Heterocarpus laevigatus*, in Hawaii. Fish. Bull. (U.S.) 84:915-925.

Gooding, R. M. 1984. Trapping surveys for the deepwater caridean shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands. Mar. Fish Rev. 46(2):18-26.

Intes, A. 1978. Deep trap fishing in New Caledonia and adjacent islands. Preliminary experiments (Peche profonde aux casiers en Nouvelle Caledonie et iles adjacentes. Essais preliminaires.) O.R.S.T.O.M. (Noumea) Rapp. Sci. Tech. 2, 10 p.

King, M. G. 1980. A trapping survey for deepwater shrimp (Decapoda: natantia) in Western Samoa. Rep. Inst. Mar. Resour., Univ. South Pac., Suva, Fiji, 26 p.

________. 1981a. Deepwater shrimp resources in Vanuatu: A preliminary survey off Port Vila. Mar. Fish. Rev. 43(12):10-17.

________. 1981b. The deepwater shrimps of Tonga: A preliminary survey near Nuku'alofa. Rep. Inst. Mar. Resour., Univ. South Pac., Suva, Fiji. 28 p.

________. 1982. Report on the South Pacific Commission deepwater shrimp assessment consultancy in Papua New Guinea. South Pac. Comm., Noumea, New Caledonia, 24 p.

________. 1984. The species and depth distribution of deepwater caridean shrimps (Decapoda, Caridea) near some southwest Pacific islands. Crustaceana 47(2):174-191.

________. 1986. Fishery resources of Pacific island countries. Part 1. Deepwater shrimps. FAO Fish. Tech. Pap. 272.1, 45 p.

Moffitt, R. B. 1983. *Heterocarpus longirostris* MacGilchrist from the Northern Mariana Islands. Fish. Bull. (U.S.) 83:434-436.

________ and J. J. Polovina. 1987. Distribution and yield of the deepwater shrimp *Heterocarpus* resource in the Marianas. Fish. Bull. (U.S.) 85:339-349.

Ralston, S. 1986. An intensive fishery experiment for the caridean shrimp *Heterocarpus laevigatus* at Alamagan Island in the Mariana Archipelago. Fish. Bull. (U.S.) 84:927-934.

________, R. M. Gooding, and G. M. Ludwig. 1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. Fish. Bull. (U.S.) 84:141-154.

Saunders, W. B. 1984. The role and status of Nautilus in its natural habitat: Evidence from deep-water remote camera photosequences. Paleobiology 10:469-486.

Schlais, J. F. 1982. Deepwater shrimps, a new Pacific fishery. Sea Frontiers, Nov.-Dec.

________. 1983. Fledgling Hawaiian shrimp fishery could someday rival the Gulf catch. Natl. Fisherman 64(3):8.

Struhsaker, P., and D. C. Aasted. 1974. Deepwater shrimp trapping in the Hawaiian Islands. Mar. Fish. Rev. 36(10):24-30.

Wilder, M. J. 1977. Biological aspects of the fisheries potential of two deep water shrimp, *Heterocarpus ensifer* and *H. laevigatus* in waters surrounding Guam. M.S. Thesis, Univ. Guam, 79 p.

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# MARINE DEBRIS IN HAWAII

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# INTRODUCTION

The production and use of plastics and other synthetic materials have increased rapidly in recent decades. With this increase, a growing problem has arisen of plastic debris polluting the environment. Because of the aesthetic effect of litter on the terrestial environment, improper disposal of plastics on land has been an issue for some time. Only in recent years, however, have the effects of plastic debris in the marine environment become more vivid (Shomura and Yoshida 1985; Laist 1987). Seabirds and sea turtles can ingest pieces of plastic that block or impede their digestive tracts; marine mammals, seabirds, and fish can become entangled in fragments of trawl webbing or gill net; also, floating rope or webbing can disable vessels by fouling propellers.

With a relatively small human population and no extensive industrial sources of effluent plastic particles, Hawaii is not faced with many of the marine debris problems encountered along continental margins. Also, plastic litter generated in Hawaii may be borne away on oceanic currents rather than remain near shore. Yet because of its midocean location (Fig. 1), Hawaii is recipient of flotsam and debris from perhaps more widespread sources than continental coastlines. Moreover, the same current system which carries debris away from the islands also carries debris from the various fisheries of the North Pacific Ocean toward Hawaii (Pickard 1963). This debris affects the inhabitants and wildlife of Hawaii.

In the main Hawaiian Islands, state and county parks and populous beaches, such as Waikiki, are routinely cleaned of litter and marine debris by local government agencies, but data on such debris items are not collected. In the Northwestern Hawaiian Islands (NWHI), personnel of the National Marine Fisheries Service (NMFS) have since 1982 retrieved, cataloged, and burned nets, webbing, lines, and other debris that could entangle wildlife. Data collected included location, size, and estimated weight of debris. Color, twine diameter, and mesh size were also noted from net or webbing fragments. Except for plastic hoops or rings capable of encircling a seal's muzzle, the cleanup has not included other debris items such as plastics and glass.

## TYPES AND SOURCES OF DEBRIS

Although types of debris and beach litter are not regularly noted in the main Hawaiian Islands, results of a single-day beach cleanup in 1984 showed that plastic bags, cups, and utensils predominate in beach litter, with styrofoam cups,fishing lines, and ropes contributing significantly.[1] The probable sources of these items were not noted.

Despite the fact that large plastics and other flotsam not capable of entangling animals are not collected or cataloged in the NWHI, some conclusions are possible based upon many observations of plastics along the beach perimeter of these islands. Land-generated items such as six-pack yokes, styrofoam food and beverage containers, and plastic utensils are seldom seen. Rather, plastic items tend to include beverage crates, buckets, and fish baskets. This debris appears to originate from ships rather than from coastal litter. Also present on the islands are countless, small pieces of plastic resulting from the breakdown of larger plastic items. These pieces and the myriad plastic bottle caps and disposable cigarette lighters probably originate from shore. Fry et al. (1987) note that plastic trash is more abundant in the NWHI than on other remote islands in the central Pacific, and speculate that it is carried by the Kuroshio Extension into the North Pacific gyre. Seabirds that have ingested plastics may also contribute to debris in the NWHI by transporting items to the nesting area to feed their young.

Henderson et al.(1987[2]) have documented the physical characteristics of 632 samples of webbing collected from NWHI locations: 539 (85.3%) were constructed of polyethylene or polypropylene and were considered to have originated from trawl nets; 66 (10.4%) were monofilament gill nets; the remaining 27 (4.1%) were of other materials or unknown origin. Of the trawl net fragments, 17 (3.2%) were assessed to be cod ends of groundfish trawls, based on criteria of at least 6-mm twine diameter combined with stretched mesh size of 80-130 mm. The gill-net samples were assigned to probable source fisheries according to mesh size (Table 1).

It is interesting that, of the two fisheries which are the source of most of the derelict nets found in Hawaii, the trawl fishery contributes most of the material. This is despite the fact that the squid gill-net fishery operates closer to Hawaii, and that according to some estimates (Fredin 1985; Shima 1985) the amount of gill net (both salmon and squid) involved in fishing the North Pacific far exceeds that of trawl net.

A large number of ropes and lines are found in the NWHI, but the amounts have not been quantified. These items undoubtedly originate from ships at sea.

## DISTRIBUTION OF DEBRIS ON BEACHES

Henderson et al. (footnote 2) described the distribution of derelict trawl web and gill net on the shores of the NWHI. Netting tends to wash ashore on beaches facing northeast, beaches exposed to the northeasterly trade winds which are predominant most of the year. Certain promontories along islands also accumulate debris as a result of inshore currents. At French Frigate Shoals, a multi-islet atoll, debris accumulates more on Trig, Whale-Skate, and East Islands, the three more permanent and vegetated islands within the atoll. Trig and Whale-Skate Islands are on the windward (northeast) edge of the atoll, whereas East Island is on the leeward (western) perimeter. The uneven distribution of nets presents a particular hazard to Hawaiian monk seals, Monachus schauinslandi, at Lisianski Island and French Frigate Shoals. At Lisianski Island, pups are born predominantly on the east side of the island (Johanos and Henderson 1986; Johanos and Kam 1986), coincident with areas of higher debris accumulation. At French Frigate Shoals, a major pupping site for seals, approximately one-half of all seal pups born in 1983 were born on East and Whale-Skate Islands, two of the islands accumulating the most debris.

## ENTANGLEMENT IN MARINE DEBRIS

Debris items may possess openings capable of ensnaring marine animals. Depending on the size of the item, an entangled animal will be either immobilized or able to continue its movements while "wearing" the debris. In the latter instance, eventual death may result as the animal "grows into" the debris item. Animals in Hawaii that are known to become entangled include marine mammals, sea turtles, seabirds, and fish.

## Marine Mammals

The Hawaiian monk seal is endemic to Hawaii and is the only pinniped that regularly occurs there. Virtually all marine mammal entanglements in Hawaii have involved monk seals. Thirty-five incidents of monk seal entanglement have been documented in Hawaii through 1984, including eight seals bearing scars indicative of a previous entanglement from which the animal had escaped (Henderson 1985). From 1985 through 1987, 19 monk seals were observed entangled or bearing new scars from recent entanglements (Henderson unpubl. data). Among these incidents were three deaths. One weaned pup died in 1986 after becoming entangled in wire debris at East Island, French Frigate Shoals. In 1987, two seals died after becoming entangled in large fragments of trawl web which previously had washed ashore: A yearling died at Shark Island, French Frigate Shoals, and a pup died at Lisianski Island. The 19 incidents over 3 years represent an increase in entanglement rate since 1984. In 1983-84, eight incidents were noted (Henderson 1985). This increase has occurred despite the fact that beaches in the NWHI are cleaned at least annually of debris that might entangle animals.

One entanglement incident has been reported involving cetaceans in Hawaii. In January 1987, a humpback whale, _Megaptera novaeangliae_, was sighted between Lahaina, Maui, and the Island of Lanai, towing an orange buoy of unknown origin (L. Consiglieri pers. commun.[3]). The animal was sighted only once, and its ultimate fate is unknown. It is possible that the buoy had been towed a long distance; gray whales, _Eschrichtius robutus_, have been documented in Washington, towing nets picked up in California (Beach et al 1985[4]).

## Sea Turtles

Twenty-five incidents of sea turtle entanglement through 1984 have been documented, including 20 green turtles, *Chelonia mydas*; 4 olive ridley turtles, *Lepidochelys olivacea*; and 1 hawksbill turtle, *Eretmochelys imbricata* (Balazs 1985). One of the entangled green turtles was a hatchling entrapped while moving toward the sea soon after hatching. The cases of entangled olive ridley turtles are noteworthy in that they comprise most of the documented occurrences of this species in Hawaii. It is likely that the animals became entangled in their normal range to the south of Hawaii and passively drifted north.

## Seabirds

The NWHI are a nesting location for approximately 5.4 million seabirds (Fefer et al. 1984), and several species have been observed entangled. An immature masked booby, *Sula dactylatra*, was found entangled in a scrap of trawl net on Nihoa Island (Conant 1984), and black-footed albatross, *Diomedea nigripes*; Laysan albatross, *D. immutabilis*; and sooty terns, *Sterna fuscata*, have also been observed entangled (S. Fefer pers. commun.[5]). The NWHI are a nesting location for approximately 5.4 million seabirds (Fefer et al. 1984), and several species have been observed entangled.

## Fish

Few reports exist of fish becoming entangled in marine debris in Hawaii. An ulua, *Caranx* sp., was found entangled in a large pile of trawl net which was fouled on an offshore reef at Lisianski Island (Henderson 1984). The author has also observed several dead parrotfish, *Scarus* sp., entangled in a derelict barrier net on Oahu, and a dead ulua caught by a pile of trawl net on Seal-Kittery Island, Pearl and Hermes Reef. A large mass of trawl and gill net retrieved for the shallow lagoon at Kure Atoll contained skeletal remains of at least four fish, tentatively identified as billfish (family Istiophoridae), tuna (family Scombridae), and barracuda (family Sphryaenidae) (M. Seki pers. commun.[6]).

It is difficult to determine whether fish found in derelict fishing gear were caught while the net was actively fishing or after it was lost. Abandoned barrier nets will continue to catch fish for many years (High 1985).

## Passerine Birds

Although this description does not report entanglement, one impact of debris on an endemic passerine bird is noteworthy. Morin (1987) reported deaths in marine debris of the Laysan finch, _Telespyza cantans_, which is endemic to Laysan Island in the NWHI. During dry summer months, fresh water is scarce on Laysan, causing birds to seek water whenever or wherever available. Certain debris items, such as broken plastic fishing floats or plastic crates, form cisterns for rainwater. In 1986, two Laysan finches drowned in a plastic cooler, having apparently been unable to escape after venturing in to drink the fresh water. The cooler was high on the beach and had evidently been washed ashore for some time. Although this may have been a rare occurrence, the potential exists for loss of more birds under similar circumstances.

## INGESTION OF MARINE DEBRIS

Marine debris may be ingested because it resembles the natural food items of certain species or may be ingested during normal feeding on natural food. Plastic spherules resemble fish eggs, and plastic bags or balloons resemble coelenterates. Plastic flotsam also provides a substrate on which flyingfish (family Exocoetidae) lay eggs, and animals feeding on the eggs may also ingest the plastic. Furthermore, some marine animals are opportunistic feeders, eating anything of a suitable size found floating on the ocean surface, including plastics. Potential effects of ingested debris include intestinal blockage, physical debilitation or starvation resulting from a reduced feeding drive due to the presence of debris in the stomach, poisoning from compounds which leach from the plastic, or perforation of the gastrointestinal wall. Animals in Hawaii that are known to ingest plastic or other debris include cetaceans, sea turtles, and seabirds.

### Cetaceans

A single occurrence of a cetacean ingesting debris has been noted in Hawaii. A clear plastic trash bag was found in the stomach of an immature male Risso's dolphin, Grampus griseus, which stranded on Maui in February 1988 (E. Nitta pers. commun.[7]). It is not known whether the bag caused or contributed to the death of the animal.

### Sea Turtles

Seven cases of ingestion of plastic by sea turtles in Hawaii have been reported through 1984, six of which involved the green turtle and one of which involved the hawksbill turtle (Balazs 1985). The majority of green turtles found to ingest plastic were juveniles. Juvenile turtles live a pelagic existence for perhaps several years after hatching before returning to the nearshore areas to feed on benthic algae. During pelagic existence, their normal diet consists of floating items such as coelenterates, algae, and pelagic mollusks (Carr and Meylan 1980), and turtles are more likely to encounter and ingest debris at this early age (Carr 1987).

Turtles may in some instances be able to pass plastic materials through their gastrointestinal tract and expel them. One young green turtle, which was being maintained in captivity, ingested a plastic bag, part of which was found protruding through the cloaca. Dead turtles have also been found with shreds of plastic bags in the feces in the lower intestine, suggesting that the bags may not always obstruct the digestive tract.

## Seabirds

Ingestion of plastics is ubiquitous among seabirds breeding in Hawaii. In a study of plastic ingestion by nestling seabirds at Midway Islands, 14 of 16 species were found to have ingested plastic (P. Sievert pers. commun.[8]). Young birds are more likely to ingest plastic because they are fed regurgitated food by the parent and tend to accumulate indigestible items.

The effects of ingested plastics on young seabirds are unclear. Many hard items, such as pumice, squid beaks, and floating seeds, naturally occur in seabird diets; hence, young birds have evolved means of casting such residue, including plastics. Healthy albatross chicks, for example, naturally regurgitate hard items that have become concentrated in the proventriculus. Chicks debilitated by disease or dehydration, however, may be unable to regurgitate normally and may experience higher mortality, either from the original source of debilitation, the presence of plastics, or a combination of these factors (see footnote 8).

Plastic ingestion may also occur frequently among adult Hawaiian seabirds. Birds which are surface feeders are particularly susceptible (Day et al. 1985); 90% of adult Laysan albatross examined by Fry et al. (1987) had ingested plastic items.

## EFFECTS ON HUMANS

The author knows of no reported fouling of propellers or other entanglements with vessels at sea near Hawaii that could be hazardous to human health or safety. Aesthetic degrading of beach areas is probably the most significant impact of debris on a state which depends heavily on tourism for revenue.

Marine flotsam can also have a favorable effect in Hawaii; floating pieces of trawl webbing, often called "cargo net" by local fishermen, may aggregate large fish communities. Fishermen take advantage of this focus for fish and may catch large amounts of tuna and other commercially valuable species in association with floating net fragments.

## SUMMARY

Despite, or perhaps because of, its midocean location, Hawaii is affected by the problem of plastic pollution and marine debris in the world's oceans. The remote NWHI daily are recipient of nets and other flotsam in which endangered monk seals, threatened and endangered sea turtles, and protected seabirds may become entangled. Nesting seabirds and foraging juvenile turtles range widely from the islands, ingesting plastic or other items mistaken for food. Within the main islands, derelict nets are both a danger and a boon to fishermen, who risk having their boats become fouled in abandoned webbing, yet who may also catch large amounts of commercially valuable fish associated with the flotsam. The aesthetic effect of marine debris on beaches is difficult to quantify but is certainly evident, particularly along windward beaches.

## LITERATURE CITED

Balazs, G. H.

1985. Impact of ocean debris on marine turtles: Entanglement and ingestion. In R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 387-429. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

Carr, A.

1987. Impact of nondegradable marine debris on the ecology and survival outlook of sea turtles. Mar. Pollut. Bull. 18(6B):352-356.

Carr, A., and A. B. Meylan.

1980. Evidence of passive migration of green turtle hatchlings in Sargassum. Copeia 1980:366-368.

Conant, S.

1984. Man-made debris and marine wildlife in the Northwestern Hawaiian Islands. 'Elepaio 44(9):87-88.

Day, R. H., D. H. S. Wehle, and F. C. Coleman.

1985. Ingestion of plastic pollutants by seabirds. In R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 344-386. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-54.

Fefer, S. I., C. S. Harrison, M. B. Naughton, and R. J. Shallenberger.

1984. Synopsis of results of recent seabird research conducted in the Northwestern Hawaiian Islands. In R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the second symposium on resource investigations in the Northwestern Hawaiian Islands, Vol. 1, May 25-27

1983, University of Hawaii, Honolulu, Hawaii, p. 9-76. Sea Grant Miscellaneous Rep., UNIHI-SEAGRANT-MR-84-01.

Fredin, R. A.

1985. Fishing effort by net fisheries in the North Pacific Ocean and Bering Sea since the 1950's. In R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 218-251. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

Fry, D. M., S. I. Fefer, and L. Sileo.

1987. Ingestion of plastic debris by Laysan albatrosses and wedge-tailed shearwaters in the Hawaiian Islands. Mar. Pollut. Bull. 18(6B):339-343.

Henderson, J. R.

1984. Encounters of Hawaiian monk seals with fishing gear at Lisianski Island, 1982. Mar. Fish. Rev. 46(3):59-61.

1985. A review of Hawaiian monk seal entanglements in marine debris. In R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 326-335. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

High, W. L.

1985. Some consequences of lost fishing gear. In R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 430-437. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

Johanos, T. C., and J. R. Henderson.

1986. Hawaiian monk seal reproduction and injuries on Lisianski Island, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-64, 7 p.

Johanos, T. C., and A. K. H. Kam.

1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-58, 37 p.

Laist, D. W.

1987. Overview of the biological effects of lost and discarded plastic debris in the marine environment. Mar. Pollut. Bull. 18(68):319-326.

Morin, M. P.

1987. Laysan finches drown as a result of marine debris. 'Elepaio 41(1):107-108.

Pickard, G. L.

1963. Descriptive physical oceanography. Pergamon Press, NY, 200 p.

Shima, K.

1985. Summary of Japanese net fisheries in the North Pacific Ocean. In R. S. Shomura and H. O. Yoshida (editors), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii, p. 252. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54.

Shomura, R. S., and H. O. Yoshida (editors).

1985. Proceedings of the workshop of the fate and impact of marine debris, 27-29 November 1984, Honolulu, Hawaii. U.S. Dep. Commer. NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-54, 580 p.

# FOOTNOTES

[1] City and County of Honolulu, community work day program, press release, October 28, 1987.

[2] Henderson, J. R., S. L. Austin, and M. B. Pillos. 1987. Summary of webbing and net fragments found on Northwestern Hawaiian Islands beaches, 1982-86. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-11, 15 p.

[3] L. Consiglieri, Western Pacific Program Office, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396, pers. commun. February 1987).

[4] Beach, R. J., A. C. Geiger, S. J. Jeffries, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1982-85. Processed Rep. 85-04, 316 p. Available from Northwest and Alaska Fish. Cent., Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115.

[5] S. Fefer, U.S. Fish and Wildlife Service, P.O. Box 50167, Honolulu, HI 96850, pers. commun. January 1988.

[6] M. Seki, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396, pers. commun. August 1987.

[7] E. Nitta, Western Pacific Program Office, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396, pers. commun. February 1988.

[8] P. Sievert, National Wildlife Health Laboratory, U.S. Fish Wildl. Serv., 6006 Schroeder Road, Madison, WI 53711, pers. commun. August 1987.

Table 1.--Number of gill-net fragments found on beaches of Northwestern Hawaiian Islands in 1982-85, with probable source fishery.

| Mesh size (mm) | No. | Probable source fishery |
|---|---|---|
| Unknown | 5 | Unknown |
| 15 | 1 | Soviet saury/anchovy (?) |
| 50-58 | 4 | North American coastal herring |
| 89-109 | 32 | High seas squid |
| 110-115 | 14 | High seas or Asian land-based salmon or high seas squid |
| 119-130 | 8 | High seas salmon |
| 140-160 | 2 | North American coastal salmon |

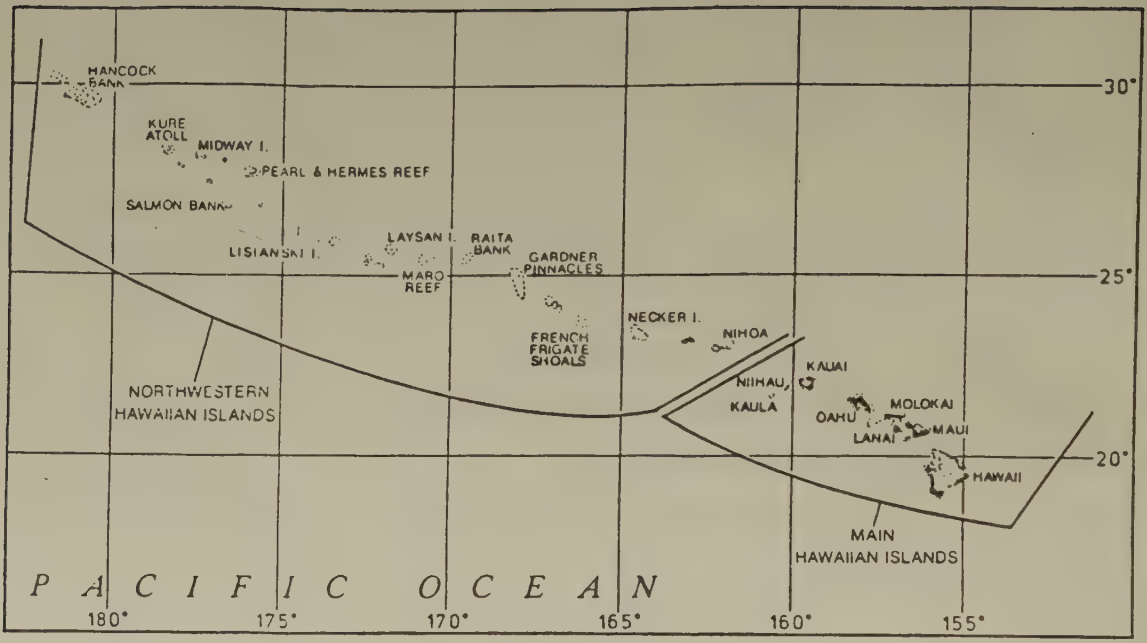
HANCOCK BANK
KURE ATOLL
MIDWAY I.
PEARL & HERMES REEF
SALMON BANK
LISIANSKI I.
LAYSAN I.
RAITA BANK
MARO REEF
GARDNER PINNACLES
FRENCH FRIGATE SHOALS
NECKER I.
NIHOA
KAUAI
NIIHAU,
KAULA
OAHU
MOLOKAI
LANAI
MAUI
HAWAII
NORTHWESTERN HAWAIIAN ISLANDS
MAIN HAWAIIAN ISLANDS
30°
25°
20°
PACIFIC OCEAN
180°
175°
170°
165°
160°
155°

Figure 1.--Hawaiian Archipelago.

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# EFFECTS OF TAGGING ON WEANED HAWAIIAN MONK SEAL PUPS

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Flipper tagging is a valuable technique in research and management of pinnipeds, providing such information as abundance, movement, age-specific survivorship, and age at first reproduction. Although this technique is usually considered to have no effect on subsequent behavior or survival of pinnipeds, some evidence exists that tagged animals are disturbed during capture and restraint and possibly by the continued presence of the tag. For example, northern fur seal (*Callorhinus ursinus*) pups suffered increased mortality for up to 1 week after capture and tagging (Roppel et al. 1963). Mammals that are prey to carnivores may react to disturbances, particularly capture and restraint, with a complex suite of behavioral and physiological responses, including "freezing" and marked bradycardia (Smith and Johnson 1984).

Even if capture and restraint are not harmful, the presence of marking devices may affect subsequent behavior or survival. Behavioral changes due to markers have been documented in birds (Burley et al. 1982, Jackson 1982) and ungulates (Queal and Hlavachick 1968, Beale and Smith 1973), but capture alone had no effect on subsequent reproductive success of adult female deer (Hamlin et al. 1982). Tags that affect foraging ability may cause increased mortality, an effect difficult to detect or to attribute to tags unless a control group is tested. Northern fur seal pups tagged and then marked with flipper notches had a lower survival rate over 2 years than did animals that were only marked (U.S. Natl. Mar. Fish. Serv. [NMFS] 1970).

Counts of the Hawaiian monk seal (*Monachus schauinslandi*) indicated a population decline of about 50% since 1958 (Johnson et al. 1982). Human disturbance, including biological research, is one of several factors contributing to this decline (Kenyon 1972). In the 1950's, some nursing pups and their mothers were tagged, and the pups were weighed periodically (Kenyon and Rice 1959, Wirtz 1968), but the extent to which these procedures affected the seals is not known. Because of potentially adverse effects of "hands-on" research, our study assessed the combined short-term effects of capture, restraint, and tagging on behavior and survival of weaned monk seal pups.

## STUDY AREA AND METHODS

The study was initiated in spring 1982 on Lisianski Island, a low, sandy, 1.8-km² area about 1,700 km northwest of Honolulu, Hawaii. Beaches and rocky ledges comprise the island's 5.25-km perimeter. The island and surrounding shoals were inhabited by a relatively closed population of about 215 monk seals (Stone 1984). Pups were born from February to July, with peak births occurring from March to May.

### *Marking and Tagging*

In 1982 we marked monk seal pups with identifying numbers on their pelage by commercial hair bleach (LeBoeuf and Peterson 1969). Bleach was applied 1–4 days after weaning while the pups were asleep, causing no apparent disturbance. Three pups that had weaned before the field party's arrival on 18 March were marked on 20–21 March. One or 2 days after bleach-marking, we also tagged 50% of the marked pups with a dark green plastic Temple Tag® between the fourth and fifth digit of each rear flipper. Tagging required capturing and restraining the pups by hand for 5–15 minutes. Tagging procedures followed Gilmartin et al. (1986), except that we inserted a metal screw through the trailing portions of the tag, a procedure that required most of the restraint time. We defined marking dates as the dates of tagging for tagged pups and of bleaching for untagged pups. Pups were classed by time after marking into 16 successive, 2-week strata, and data were analyzed by strata. The last pup to wean was marked on 27 July and was in stratum 4 (8–10 weeks after marking) when the study was completed. Thus, all pups contributed to observations through stratum 4, with progressively fewer pups observed at the later strata. We assigned randomly every other pup weaned to the tagged or untagged group, and the next pup to wean was assigned to the opposite group without regard to sex of pups in tagged versus untagged groups. Twenty-six pups survived to weaning on Lisianski Island in 1982 (Stone 1984); 13 (7 M, 6 F) were marked and tagged, and 13 (8 M, 5 F) were marked only. The Mann-Whitney *U*-test (Conover 1971) was used to determine whether tagged and untagged pups were marked at similar or dissimilar sites.

### *Presence and Location on Island*

We determined locations of pups during 21 March–13 September and 26 October–22 November by ≥2 observers walking the perimeter of the island at least twice daily (i.e., min. of 4 circuits, except for single circuits on 3 separate days). The daily time of circuits varied, but generally occurred from early daylight to dusk. We divided the perimeter into 49 sectors of about equal length, and considered the daily location of each pup to be the sector in which it was first sighted. Pups not seen were assumed to be at sea until resighted. The Chi-square test was used to test for differences in number of days that tagged and untagged pups were present on the island.

Statistical tests between the 2 groups of seals were applied separately by stratum because observations at different strata are not independent of each other. This procedure, however, is analogous to multiple sampling, a process in which statistically significant results may arise because of chance when any test is repeated many times.

Trips at sea that overlapped strata were assigned to the stratum with the majority of trip days. If 2 strata included equal numbers of trip days, we assigned the trip to the later stratum. Data on length and number of trips from the island were constrained temporally (min. trip length = 1 day, max. No. of trips/stratum = 7) and were not normally distributed. The Wilcoxon nonparametric test (Conover 1971) was used to test for differences in median number of trips and median trip length between tagged and untagged pups.

Number of sectors between marking and haul-out locations could be determined because locations of pups were recorded. We considered such distances to represent the shortest distance along the island's perimeter. The actual movement of pups cannot be inferred from successive locations because specific routes were not known. Thus, these data reflect only the distance from a hauling site to a marking site, with the maximum distance being half of the island perimeter (i.e., approx 24 sectors). Like the trip data, these values are not normally distributed. We used the Wilcoxon test to test for differences in distance from marking sites to haul-out sites between tagged and untagged pups.

### *Behavior and Mortality*

We observed behavior of pups on alternate days from 24 March to 13 September. Individual pups could not be identified in the nearshore water at night; hence, all observations were conducted during daylight hours. Three 2-hour observation periods (0900–1100, 1230–1430, 1600–1800) were established, each divided into 4 observation windows of 15 minutes each. We used the remainder of each period to locate particular pups. Because 3 observers simultaneously worked each period, 12 windows/period were available. For each period, pups were assigned randomly to a particular observer and window. We first observed pups marked <2 weeks earlier; pups marked ≥2 weeks earlier filled the remaining windows. Midway through the study, pups marked >10 weeks earlier were excluded from behavioral observations because they were frequently at sea.

Any pup not located by the assigned observer during the assigned window could be observed during any window in the period by any observer. Pups not located during the entire period were scored as "not found," and the numbers of tagged and untagged pups so scored were compared through stratum 5 using the Chi-square test.

Observers used stopwatches to measure the duration of 14 behavioral categories describing the pups' activity ashore and in inshore reef areas. Aquatic categories included investigating potential forage items, interacting with conspecifics, and other nondirected swimming. Categories ashore included movement, attempted nursing, awake but not moving, and asleep. We considered an awake animal to have begun sleeping when its eyes were closed for at least 30 seconds, and vice versa for a sleeping animal. Proportion of time spent per behavioral category was calculated for each pup, and values were normalized with an arcsine square-root transformation. We made no a priori assumptions as to which behaviors might differ between groups, and all behavioral categories were compared simultaneously by Hotelling's $T^2$-test (Harris 1975).

We used the Chi-square test to test any differences in numbers of deaths or disappearances between tagged and untagged seals.

## RESULTS

### *Movements and Behavior*

We saw pups on the island >90% of the days within 9–10 weeks after marking; then the percentage dropped notably (Fig. 1). The

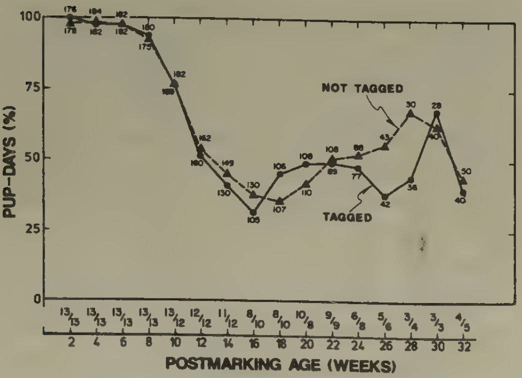

Fig. 1. . Percentage of pup-days (presence of tagged and untagged Hawaiian monk seal pups) on Lisianski Island, Hawaii, March–November 1982. Points are means; numbers are total pup-days. Number bar indicates numbers of tagged (top) and untagged (bottom) pups contributing to data.

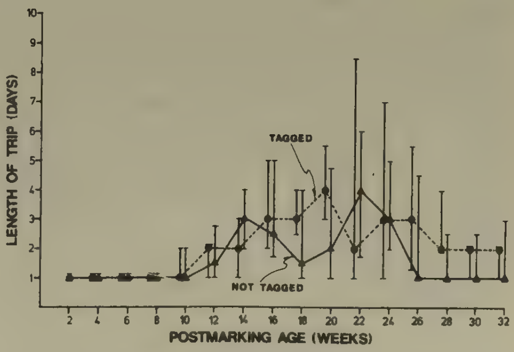

Fig. 2. Duration of trips from Lisianski Island, Hawaii, by tagged and untagged Hawaiian monk seal pups, March–November 1982. Points are medians; bars are 25–75 percentiles.

numbers of pup-days (days when seals were present on the island) for each 2-week stratum did not differ ($P > 0.07$) between tagged and untagged pups. Comparison of pups scored as "not found" during behavioral observations indicated that both groups were equally likely to be away from the island ($P = 0.83$ for strata 1–5).

Median trip length did not differ between tagged and untagged pups ($P > 0.08$ for all strata) (Fig. 2). The median number of trips did not differ between groups ($P > 0.17$ for all strata).

During the first 2 weeks after marking, tagged pups hauled out farther from their marking site than did untagged pups ($P = 0.01$) (Fig. 3). Conversely, tagged pups hauled out closer to their marking site ($P < 0.01$) 12, 14, 18, and 20 weeks after marking. No significant differences existed at the other 10 strata. Location of marking sectors about the island did not differ between groups ($P = 0.57$).

Behavioral observations of pups totaled 447 hours (223 hr for tagged pups, 224 hr for untagged pups). Behavior of tagged pups did not differ from that of untagged pups ($P > 0.25$) (Fig. 4). However, we observed 2 cases of interspecific behavior relating to the presence of tags. In both instances a swimming pup was harassed briefly by a great frigatebird (*Fregata minor*) that dove at the pup and picked at the tags. The only response by each pup was an open-mouthed threat toward the bird.

### *Mortality, Disappearance, and Tag Loss*

No mortality of tagged pups occurred during or immediately following tagging. One animal died 88 days after tagging; it was found 2 hours after being observed and was being vigorously defended by an adult male. Postmortem examination did not reveal the cause of death, although fat vacuoles noted during histological examination of liver tissue suggested protein malnutrition. A second tagged seal disappeared in late September or early October, about 7 months after tagging (Stone 1984). As of August 1987, this seal had not been resighted at any location and was presumed dead (Southwest Fish. Cent. Honolulu Lab., NMFS, unpubl. data).

The remaining 11 tagged seals were resighted in 1983 (Johanos and Kam 1986) and as recently as 1986 (R. L. Westlake, Southwest Fish. Cent. Honolulu Lab., NMFS, unpubl. data). All 13 of the untagged seals survived for >1 year (Johanos and Kam 1986), at which

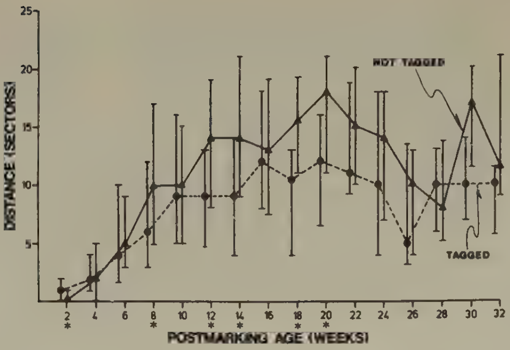

Fig. 3. Distance from marking site to haul-out site of tagged and untagged Hawaiian monk seal pups on Lisianski Island, Hawaii, March–November 1982. Points are medians; bars are 25–75 percentiles (* $P < 0.05$).

time they molted the pelage bearing the identifying bleach marks. The Chi-square test of equal mortality revealed no difference between the tagged and untagged groups ($P > 0.10$).

Of the 26 tags applied (2 each for 13 pups), one was lost during the study, and one was lost in 1985 (D. J. Alcorn, Southwest Fish. Cent. Honolulu Lab., NMFS, unpubl. data). Both tags had pulled through the flipper webbing, leaving a healed tear in the tissue.

## DISCUSSION

Tagged pups were present the same percentage of days as untagged pups, indicating handling did not cause increased time at sea. Numbers and lengths of trips from the island also were equal between groups, suggesting that tagging did not affect the normal pattern of foraging trips at sea and haul-out ashore.

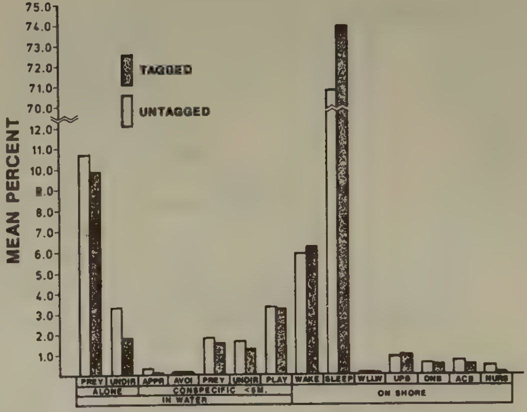

Fig. 4. Behavior of tagged and untagged Hawaiian monk seal pups on Lisianski Island, Hawaii, March–September 1982. Bars indicate percentage of time observed in each behavioral category. PREY = investigating potential forage; UNDIR = nondirected swimming; APPR = approaching conspecific; AVOI = swimming away from conspecific; PLAY = grasp, roll, or mock-fight with conspecific; WAKE = awake, unmoving; SLEEP = asleep; WLLW = wallowing in sand; UPB, DNB, ACB = move up, down, or across beach; NURS = attempt to nurse.

Disturbance induced by tagging might cause pups to avoid the area of capture, and any such effect would be expected to occur shortly after tagging. Such avoidance may account for the differences observed during the first 2 weeks after marking. Nevertheless, any effects were short term because the haul-out distance from marking sites was equal for tagged and untagged pups 4 weeks after marking. We cannot explain the finding that tagged pups hauled out closer to their marking sites at 12, 14, 18, and 20 weeks after marking. Because marking and tagging sites did not differ between groups, any consistent haul-out at a particular location by the aggregate of weaned pups would not produce the observed difference.

Systematic, detailed observations of pup behavior on shore and in the nearshore reef shallows revealed no differences between tagged and untagged groups. Behavioral changes would be expected to include attempts to remove tags or movement of the tagged flipper if irritated which, in turn, might also increase the time awake on shore because of shaking, scratching, or other movement of the rear flippers. No such behavior was observed, nor did any apparent infections result from tagging.

It is not known to what extent tagging contributed to the death or disappearance of 2 weaned pups. Both pups weaned before the field party's arrival on the island, so their nursing times or condition at weaning are unknown. The protein malnourishment of the known dead pup does not imply that tags impaired foraging. Weaned phocids undergo a prolonged fast while learning to feed. During this time, subarctic species, such as the harp seal (*Phoca groenlandica*), rely initially on core reserves of lipids and proteins as energy sources before metabolizing blubber fat later in the fast (Worthy and Lavigne 1983). Temperate species, such as northern elephant seals (*Mirounga angustirostris*), use lipids exclusively from the blubber layer (Ortiz et al. 1978). The duration of the fast is not known for monk seals, although northern elephant seals fast for at least 8–12 weeks (Ortiz et al. 1978).

The postweaning disappearance or mortality of 2 tagged pups during their first year represents 8% of the 26 weaned pups and 15% of the tagged group. The difference in mortality for the 2 groups (2 vs. 0 deaths) was not statistically significant, assuming an equal probability of 2 mortalities among the untagged group. Nevertheless, if the 2 pups had died as a result of tagging, a 15% mortality estimate might be appropriate for any group of pups tagged in the future. First-year mortality for pups tagged in 1983 at Lisianski Island was 12% (D. J. Alcorn, Southwest Fish. Cent. Honolulu Lab., NMFS, unpubl. data) and for pups tagged at Laysan Island in 1983 and 1984 was 5% (Johanos et al. 1987) and 7% (T. C. Johanos, Southwest Fish. Cent. Honolulu Lab., NMFS, unpubl. data), respectively.

Data on first-year mortality of untagged pups are sparse. Johnson and Johnson (1981) observed 14% mortality or disappearance of weaned pups on Laysan Island during the first 6 months of age. Recent beach counts at this island suggested that its population is relatively stable (Alcorn 1984). At French Frigate Shoals, first-year mortality of untagged, bleach-marked pups was about 16% from 1983 to 1984 (J. R. Henderson, Southwest Fish. Cent. Honolulu Lab., NMFS, unpubl. data). This population has apparently leveled off after several years of increase (Johnson et al. 1982). Much higher mortality rates were observed at Kure Atoll in 1964 and 1965 (Wirtz 1968), and have contributed to a subsequent decline in that population (Johnson et al. 1982). About 50% of the weaned pups of northern elephant seals die during the first 7 months after leaving the shore (Reiter et al. 1978).

In our study we attributed the 100% survival of tagged pups during the few weeks immediately after capture to both restraining the pups for a short time and not herding or driving the animals before tagging. The latter procedure caused increased mortality of northern fur seal pups (Roppel et al. 1963).

## SUMMARY

This study assessed the combined, short-term effects of capture, restraint, and tagging on weaned Hawaiian monk seal pups. Thirteen pups were tagged and marked; 13 were marked only. Pups were observed for up to 32 weeks after marking. Analyses of percentage of days seen ashore and the numbers and lengths of trips from the island revealed no differences between the 2 groups. A test of 14 behavioral categories revealed no differences in behavior. During the first 2 weeks after marking, tagged pups hauled out in locations significantly farther from marking sites than did their untagged counterparts. This effect disappeared by 4 weeks after marking, and 12, 14, 18, and 20 weeks after marking, tagged pups hauled out closer to their marking sites. First-year survival of both groups was similar, and we observed no mortality attributable to tagging. Tag loss over 4 years was 8%. Flipper tagging is a procedure that does not adversely affect weaned Hawaiian monk seal pups in the short term.

*Acknowledgments.*—We thank the U.S. Coast Guard, the officers and crew of the NOAA ship *Townsend Cromwell* and FV *Easy Rider*, and Tern Island personnel of the U.S. Fish and Wildlife Service for logistical support. Comments by D. P. DeMaster and H. S. Stone improved the manuscript, and T. Gerrodette assisted in the Hotelling's $T^2$ analysis. This study was conducted under U.S. Fish and Wildlife Service Special Use Permit HWN-3-82, and Marine Mammal and Endangered Species Permit 372.

## LITERATURE CITED

ALCORN, D. J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-42. 37pp.

BEALE, D. M., AND A. D. SMITH. 1973. Mortality of pronghorn antelope fawns in western Utah. J. Wildl. Manage. 37:343–352.

BURLEY, N., G. KRANTZBERG, AND P. RADMAN. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. Anim. Behav. 30: 444–455.

CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, New York, N.Y. 462pp.

GILMARTIN, W. G., R. J. MORROW, AND A. M. HOUTMAN. 1986. Hawaiian monk seal observations and captive maintenance project at Kure Atoll, 1981. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-59. 9pp.

HAMLIN, K. L., R. J. MACKIE, J. G. MUNDINGER, AND D. F. PAC. 1982. Effect of capture and marking on fawn production in deer. J. Wildl. Manage. 46: 1086–1089.

HARRIS, R. J. 1975. A primer of multivariate statistics. Academic Press, New York, N.Y. 332pp.

JACKSON, J. J. 1982. Effect of wing tags on renesting interval in red-winged blackbirds. J. Wildl. Manage. 46:1077–1079.

JOHANOS, T. C., AND A. K. H. KAM. 1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-58. 37pp.

———, ———, AND R. G. FORSYTH. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-70. 38pp.

JOHNSON, A. M., R. L. DELONG, C. H. FISCUS, AND K. W. KENYON. 1982. Population status of the Hawaiian monk seal (*Monachus schauinslandi*), 1978. J. Mammal. 63:415–421.

JOHNSON, B. W., AND P. A. JOHNSON. 1981. Estimating the Hawaiian monk seal population on Laysan Island. U.S. Dep. Commer., Natl. Tech. Inf. Serv., PB82-106113. 29pp.

KENYON, K. W. 1972. Man versus the monk seal. J. Mammal. 53:687–696.

———, AND D. W. RICE. 1959. Life history of the Hawaiian monk seal. Pac. Sci. 13:215–252.

LEBOEUF, B. J., AND R. S. PETERSON. 1969. Social status and mating activity in elephant seals. Science 163:91–93.

ORTIZ, C. L., D. COSTA, AND B. J. LEBOEUF. 1978. Water and energy flux in elephant seal pups fasting under natural conditions. Physiol. Zool. 51:166–178.

QUEAL, L. M., AND B. D. HLAVACHICK. 1968. A modified marking technique for young ungulates. J. Wildl. Manage. 32:628–629.

REITER, J., N. L. STINSON, AND B. J. LEBOEUF. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. Behav. Ecol. Sociobiol. 3:337–367.

ROPPEL, A. Y., A. M. JOHNSON, R. D. BAUER, D. G. CHAPMAN, AND F. WILKE. 1963. Fur seal investigations Pribilof Islands, Alaska 1962. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Fish. 454. 101pp.

SMITH, E. N., AND C. JOHNSON. 1984. Fear bradycardia in the eastern fox squirrel, *Sciurus niger*, and eastern grey squirrel, *S. carolinesis [sic]*. Comp. Biochem. Physiol. 78A:409–411.

STONE, H. S. 1984. Hawaiian monk seal population research, Lisianski Island, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-47. 33pp.

U.S. NATIONAL MARINE FISHERIES SERVICE. 1970. Fur seal investigations, 1968. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Spec. Sci. Rep.—Fish. 617. 125pp.

WIRTZ, W. O., II. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. J. Mammal. 49:229–238.

WORTHY, G. A. J., AND D. M. LAVIGNE. 1983. Energetics of fasting and subsequent growth in weaned harp seal pups, *Phoca groenlandica*. Can. J. Zool. 61:447–456.

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### Part II

# SYMPOSIUM OF THE CALCOFI CONFERENCE

### LAKE ARROWHEAD, CALIFORNIA

### NOVEMBER 3, 1987

## THE CALCOFI SAMPLING PROTOCOL AND TIME SERIES, POINT/COUNTERPOINT

What are the CalCOFI data? What was measured? How often? And where? What exactly was Wib Chapman referring to when he so often said that the California Current was the most intensively sampled piece of ocean in the world? And what do we know of its physics and its inhabitants as a result of this effort?

As the CalCOFI program approached its fortieth birthday, a symposium was convened at the 1987 CalCOFI Conference to discuss these questions. The following three papers were part of the proceedings.

In the first paper I attempt to place the CalCOFI effort in the larger context of the collapse of the sardine fishery. Scientific attention had been directed toward this fishery, once the largest in the world, since 1915. The vagaries of recruitment compounded by society's tendency to overexploit were generally recognized as coconspirators in the demise of the sardine. The CalCOFI program augmented ongoing work and marshalled additional resources to distinguish the relative influences of exploitation and the environment on the production of fish. The primary sampling tools employed at sea were the plankton net and the hydrocast bottle.

The CalCOFI data set is not homogeneous. The sampling protocol was changed several times throughout the history of the program, producing uneven temporal and spatial sample densities. I describe these sampling regimes and attempt to set them in the context of the dramatic emergence of the northern anchovy population and the response of the program's organizers.

In the next paper Joe Reid reviews the contributions of CalCOFI from the viewpoint of a physical oceanographer. Analysis of the CalCOFI data confirmed earlier descriptions of the California Current as offshore southward flow balanced by a countercurrent and upwelling. The CalCOFI surveys, when combined with large-scale surveys of the North Pacific, established broad correlations between circulation, nutrients, and zooplankton. The CalCOFI data also revealed seasonal fluctuations, aperiodic events, and eddies.

Reid notes that CalCOFI's intent was to relate variations in the circulatory pattern to changes in the biota. The first decade, however, was monotonously invariant, offering little opportunity for comparison. The steady decline in the numbers of sardines, which had started in the early 1940s, continued through this period. On the other hand, zooplankton abundance was correlated with the strength of the California Current. This correlation continued through the 1957–58 El Niño (the first major oceanographic event to be observed by the CalCOFI program) as well as through subsequent cold- and warm-water periods.

In the final paper Paul Smith and Geoff Moser review the contributions of CalCOFI from the viewpoint of biological oceanographers. Analysis of ichthyoplankton from surveys bracketing the 1957–58 El Niño revealed biogeographic patterns that moved in concert with major changes in the circulatory patterns. Recruitment to pelagic fish populations was shown to be autocorrelated over several years; trends in population abundance were shown to be autocorrelated over several decades. Contrasted with long-term temporal correlations, changes in population abundance do not appear to be concordant over the geographic range of the population.

Smith and Moser also note that recruitment to the northern anchovy population is much more variable than the anchovy's reproductive output, suggesting that prerecruit predation may control population growth. In this regard the multispecies nature of the CalCOFI data holds great potential.

With computer-aided analytical tools, trophic relationships can now be teased from the CalCOFI data set. The data, previously available only as atlases and research reports, have recently been assembled into a computer data base, and a series of ichthyoplankton data reports have been published. The data base can also be accessed through the CalCOFI On-Line Data System, making it possible for any researcher to explore the extent of the ichthyoplankton and hydrocast data, review the sampling methodology, and extract desired subsets of the data.

Still to be addressed is the future of the CalCOFI sampling program and how the sampling design can be improved to address current research questions. What should be measured, with what techniques, how often, where, and why? Would it be appropriate to develop high-speed plankton sorting and identification techniques (e.g., species-specific DNA probes, antibody assays [ELISA], and image analysis)? Would it be useful to use satellite imagery to describe the dynamics of primary production? Should we sacrifice spatial resolution and species precision for insight into temporal dynamics? And, most promising of all, should we investigate the use of genetic tools to describe population structure and the spatial dynamics of recruitment?

Whether we call it "biodynamics of the sea" or "the ecosystem approach," the essence of biological oceanography is to link the physics of the ocean with biological processes. Unfortunately, there are appallingly few demonstrations of this linkage. Walter Munk tells us that physical oceanographers are just now beginning to measure things on a scale that reflects the ocean's true variability; the implication is that biological oceanographers must do the same in order to make any sense of the world. Some linkages may prove irrelevant to the prediction of population growth. Lasker's elegant demonstrations that successful feeding by larval fish is dependent on a stable mixed layer was offset by the conclusion that survival through the larval stage was not the sole determinant of recruitment. But until we extrapolate from the individual animal and its ambit to the population and its habitat, we will be relegated to simple (and sometimes misleading) correlations between physical and biological variables.

*Roger P. Hewitt*

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# HISTORICAL REVIEW OF THE OCEANOGRAPHIC APPROACH TO FISHERY RESEARCH

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## ABSTRACT

For the last 70 years either one or both of the major clupeoid stocks off the Californias (the Pacific sardine and the northern anchovy) have been the subjects of almost continual study. This attention was stimulated by the need for information to manage the local harvest of these fishes and by the realization that the successful management of clupeoid stocks was a goal with worldwide implications.

During the 1920s, 1930s, and 1940s the California Department of Fish and Game (CDFG) conducted field studies in cooperation with the Scripps Institution of Oceanography (SIO), the California Academy of Sciences (CAS), and the U.S. Bureau of Commercial Fisheries (USBCF, now known as the National Marine Fisheries Service—NMFS). In the late 1940s, when the future of the sardine fishery became problematic, the industry funded a more intensified program of research. Endowed with an infusion of money and political support, agency scientists laid out an ambitious plan of attack.

Their plan became known as the oceanographic approach to fishery research (today we might call it an ecosystem approach) and was made synonymous with the CalCOFI program. Monthly cruises were conducted to collect plankton and water samples from a grid of stations; laboratory studies were undertaken to describe developmental stages of the young and behavior of the adults; the fishery was sampled to determine adult demography and vital rates; and new instruments and techniques were developed to enhance data collection and analyses. A more detailed understanding of the physical dynamics of the California Current and of the population dynamics of the sardine began to emerge, and the central question of the "sardine problem" came into clearer focus: What was the relative influence of exploitation versus the environment on the productivity of the sardine population?

In spite of this new understanding, the abundance of sardines declined steadily, while that of anchovies increased. The original focus of the CalCOFI program tended to diffuse, and major program reviews were conducted in 1957, 1961, and 1966. As the objectives changed, so did the field-sampling protocols.

When the state charter for the CalCOFI program ended in 1979, CDFG, SIO, and NMFS entered into an agreement to continue the field surveys, albeit on a smaller scale; to continue sponsoring annual conferences; and to continue publishing the *CalCOFI Reports* and Atlas series. The extensive time series of ichthyoplankton data, together with complementary measurements of the physical environment, constitute a major portion of the CalCOFI legacy. On-line computer display and extraction of these data is now available to the research community interested in the pelagic ecology of the California Current.

## RESUMEN

Durante los últimos 70 años, ya sea uno o ambos stocks principales de clupeidos presentes frente a California (la sardina del Pacífico y la anchoveta del Norte) han sido estudiados en forma continua. Este interés fue estimulado por la necesidad de obtener información para el manejo de la producción local de estos peces y por el reconocimiento que el manejo exitoso de los stocks de clupeidos es un objetivo con implicaciones mundiales.

Durante las décadas de 1920, 1930, y 1940, California Department of Fish and Game (CDFG) llevó a cabo estudios de terreno en cooperación con Scripps Institution of Oceanography (SIO), California Academy of Sciences (CAS), y U.S. Bureau of Commercial Fisheries (USBCF, ahora conocido como National Marine Fisheries Service—NMFS). A fines de la década de 1940, cuando el futuro de la pesquería de la sardina se tornó problemático, la industria respaldó económicamente un programa de investigación más intenso. Ayudados por una infusión de dinero y apoyo político, los científicos de estas agencias prepararon un ambicioso plan de ataque.

Este plan se hizo conocido como el enfoque oceanográfico en investigación pesquera (hoy en día probablemente denominado enfoque de ecosistema) y fue hecho sinónimo del programa CalCOFI. Se efectuaron cruceros mensuales para colectar plancton y muestras de aguas en una red de estaciones; estudios de laboratorio fueron completados con el fin de descubrir los estadíos de desarrollo de los juveniles y el comportamiento de los adultos; la pesquería fue muestreada para determinar la demografía y las tasas vitales de los adultos; nuevos instrumentos y technologías fueron desarrollados para mejorar tanto la colección de datos como el análisis delos mismos. Un entendimiento más preciso de la dinámica poblacional de la sardina comenzó a emerger, y la pregunta central del "problema de la sardina" se definió: "Cuál es la influencia relativa del hombre en comparación con la del ambiente sobre la producción de la población de la sardina?"

A pesar de este nuevo entendimiento, la abundancia de las sardinas disminuyó continuamente, mientras que la de las anchovetas aumentó. El objetivo original del programa CalCOFI se volvió difuso y, como consecuencia, importantes reevaluaciones del programa ocurrieron en 1957, 1961, y 1966. A medida que cambiaban los objetivos, cambiaron los programas de muestreo en terreno. Cuando el apoyo del estado para el programa de CalCOFI terminó en 1979, CDFG, SIO, y NMFS acordaron continuar los programas de muestreo, aunque a menor escala, al igual que el apoyo a las conferencias anuales, y a la publicación de las serie de Reports y Atlas de CalCOFI. La extensa serie de tiempo de datos ictioplanctónicos, junto con las mediciones complementarias de parámetros físicos constituyen una parte importante del legado de CalCOFI. Estos datos están ahora disponibles a través de computadoras para el uso por la comunidad de investigadores interesados en la ecología pelágica de la Corriente de California.

## INTRODUCTION

Welcome to the symposium of the 1987 CalCOFI Conference. We're here today to discuss the heart of CalCOFI: the 37-year time series of data collections—its extent, utility, and, ultimately, its value. The California Current has been referred to as the most intensively studied piece of ocean in the world. This reputation is enjoyed for two reasons: one, because the large number of marine institutions located along the coast of North America have each conducted many and varied field research programs; and two, because of the CalCOFI program.

The CalCOFI program was initiated to determine what happened to the sardines—the population declined rather precipitously in the 1930s and 1940s—and to determine the relative influences of exploitation and the environment on that decline. I will describe what was sampled, how often, over how large an area, and for what reason; that is, the extent of the CalCOFI data. Other speakers will describe the data's usefulness in depicting physical and biological processes.

In addition, we hope to encourage discussion on how the sampling design may be improved to address current research questions. Consideration should be given to new tools, new techniques, the geographic coverage, and how frequently we should make observations. We also wish to encourage discussion of a more fundamental question: Do we understand the California Current well enough now to abandon these large-scale surveys in favor of more focused research, or will we always need large-scale surveys to provide a context for our field experiments and to monitor trends and low-frequency variability? And a final question is: Have we exhausted the information content of this time series, or is there more to learn?

## EARLY SARDINE RESEARCH

Research on the California sardine began in the early part of this century. There was an explosive demand for canned sardines starting in 1915, as well as an increasing high return for sardine meal and oil. At the same time the mechanization of the fishing fleet allowed boats to venture farther offshore. Salmon and albacore were targeted first, and then the sardine. The California Fish and Game Commission, founded in 1870, was well funded and respected by the turn of the century.

In 1915, the Commission established the Department of Commercial Fisheries under N. B. Scofield. He was originally recruited to study the albacore, and he immediately hired W. F. Thompson to look at the sardines. Thompson set up the nation's first state-operated fisheries laboratory. He began a systematic collection of landing statistics, known from then on as the "pink tickets." He also trained several fisheries biologists who went on to work in the federal government—people such as Elmer Higgins and Oscar Sette.

In 1920, Thompson published a plan for studying the sardine. He was concerned about both stock overfishing and growth overfishing. But more important, he was concerned about the synergistic effects of the environment and harvest on the population. In 1929 and 1932, the Department of Commercial Fisheries collaborated with Hopkins Marine Station and conducted oceanographic and biological surveys of the early life stages of sardines. In 1937 the Department collaborated with Scripps to study surface currents off southern Cal-

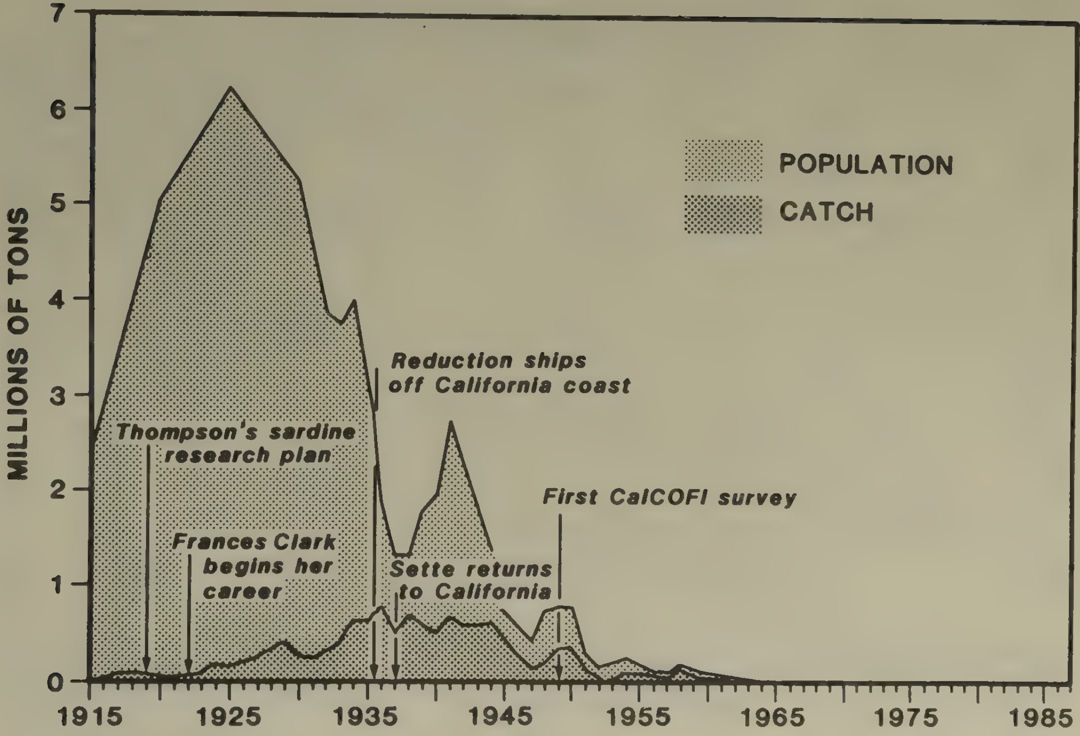

Figure 1. Pacific sardine abundance and commercial catch, since 1915 (from McEvoy 1986).

ifornia. But by the late 1920s, both Scofield and Frances Clark, who by this time had replaced Thompson, were concerned about depletion. They felt they were unable to control the fishery; the catch per unit of effort was down; and there were few older fish. In 1936 several bills were introduced to the U.S. Congress to prohibit offshore reduction ships, which were landing sardines outside the three-mile limit of California waters and reducing the fish to meal. At this time the harvest approached 790,000 tons per year. Congress asked the U.S. Bureau of Commercial Fisheries what it thought of the proposal, and Higgins, who was director at the time, refused to prohibit reduction ships on the grounds that there was insufficient evidence to curtail the commercial enterprise. The situation was further complicated in the late 1930s when there were several good year classes and the stock appeared to be recovering (Figure 1).

From 1937 through 1941 a series of ichthyoplankton cruises was conducted (Figure 2). The California Department of Fish and Game, the U.S. Bureau of Commercial Fisheries, and the Scripps Institution of Oceanography jointly participated in these cruises, which were conducted in the Southern California Bight—that is, between Point Conception and the international border. As a result of the sardine fishery's having been brought to the attention of Congress, the federal government decided to send Oscar Sette to California. Sette contributed to these cruises and eventually published a plan to determine how fishing affected the resource (Sette 1943). This plan is noteworthy because it considers all life stages of the sardines (Figure 3).

By this time, however, older fish were disappearing, and mortality was very high. With the onset of World War II, Sette was given full authority to set sardine quotas. There was a high demand for fish, and in September 1945 there were record sardine landings at Monterey. In October 1945, only one month later, the northern fishery completely collapsed. Steinbeck (1954) described this time by writing: "the canneries themselves fought the war

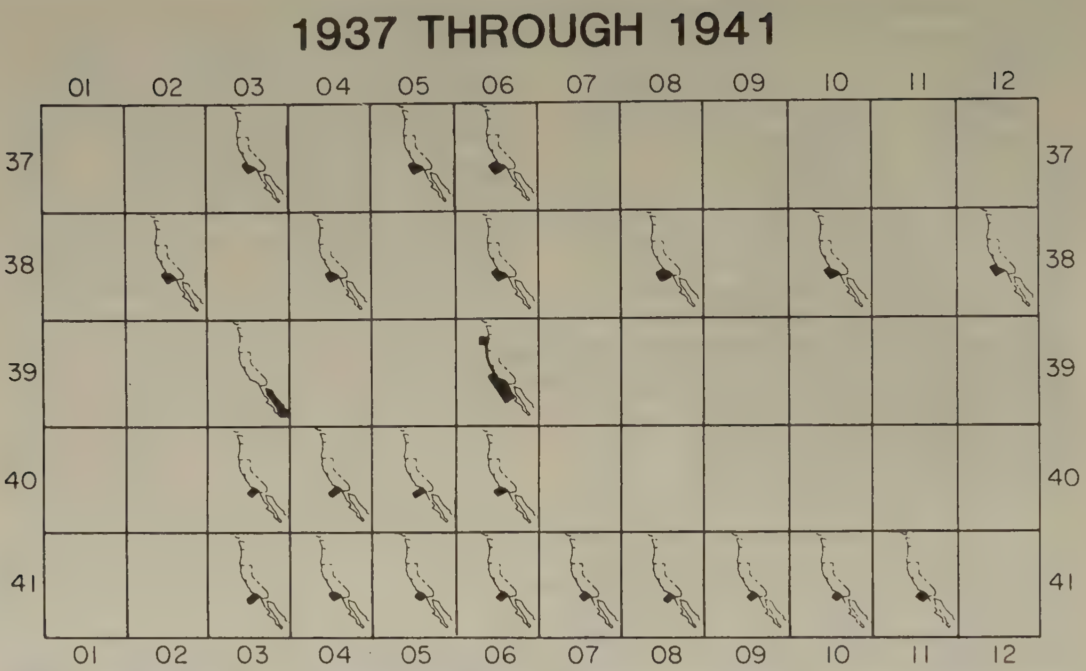

Figure 2. Ichthyoplankton cruises, 1937–41, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

by getting the limit taken off the fish and catching them all. It was done for patriotic reasons, but that didn't bring the fish back."[1]

There were a few moderately successful spawnings after the war, but 1949 through 1951 produced reproductive failures, and the southern fishery was dead by 1952. As the sardine catches declined in the late 1940s, industry leaders became increasingly alarmed. They wanted a more coordinated focus among the several agencies that were independently working on the sardine.

## CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

At the same time, Governor Earl Warren established several committees to aid industry after World War II. Robert Sproul, president of the University of California, headed one of these committees on natural resources. An informal meeting was convened at the California Academy of Sciences to discuss the problems of the sardine industry. The industry—that is, the canners—wanted help, but they weren't sure how to go about getting it. Sproul's representative was willing to put a big item in the university budget, but only if the U.S. Bureau of Commercial Fisheries and the California Department of Fish and Game cooperated. He further conditioned that the industry would have to tax itself for a matching set of funds, and stipulated that the research could not be dictated by the industry. The industry responded that it would lobby the legislature for a landing tax to be spent solely on ocean research. It wanted these expenditures, however, to be governed by a board made up of industry representatives (the Marine Research Committee). The scientists themselves, from state, federal, and academic agencies, agreed to cooperate and to form a technical committee to guide the research. Each agency, however, insisted that it would govern its own research using its own money. The governor's representative agreed to all of this, only if it was in accordance with a law passed by the legislature, and only if the governor had the authority to appoint the Marine Research Committee. Thus began a tentative confederation

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[1] Art McEvoy (1986) quoted this same passage, which succinctly captures the last major blow to the sardine population.

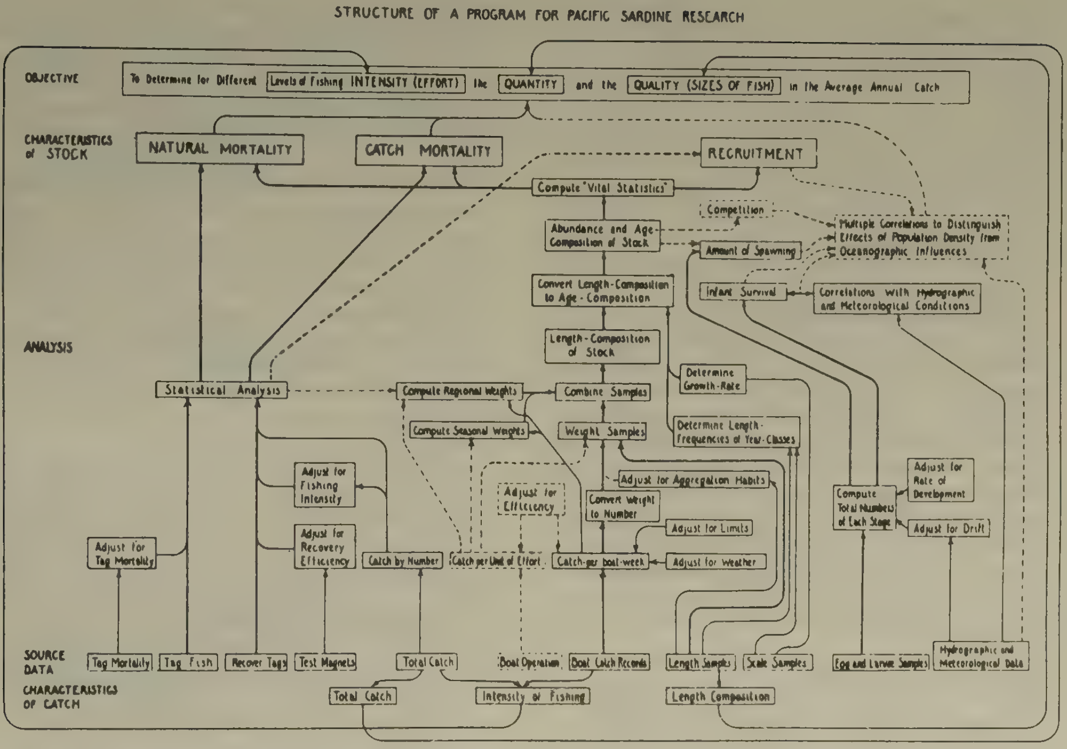
STRUCTURE OF A PROGRAM FOR PACIFIC SARDINE RESEARCH
OBJECTIVE
To Determine for Different Levels of Fishing INTENSITY (EFFORT) the QUANTITY and the QUALITY (SIZES OF FISH) in the Average Annual Catch
CHARACTERISTICS of STOCK
NATURAL MORTALITY
CATCH MORTALITY
RECRUITMENT
Compute "Vital Statistics"
Competition
Abundance and Age-Composition of Stock
Amount of Spawning
Multiple Correlations to Distinguish Effects of Population Density from Oceanographic Influences
Convert Length-Composition to Age-Composition
Infant Survival
Correlations with Hydrographic and Meteorological Conditions
ANALYSIS
Length-Composition of Stock
Determine Growth-Rate
Statistical Analysis
Compute Regional Weights
Combine Samples
Compute Seasonal Weights
Weight Samples
Determine Length-Frequencies of Year-Classes
Adjust for Fishing Intensity
Adjust for Efficiency
Adjust for Aggregation Habits
Convert Weight to Number
Adjust for Rate of Development
Compute Total Numbers of Each Stage
Adjust for Recovery Efficiency
Adjust for Tag Mortality
Adjust for Limits
Adjust for Drift
Catch by Number
Catch per Unit of Effort
Catch-per boat-week
Adjust for Weather
SOURCE DATA
Tag Mortality
Tag Fish
Recover Tags
Test Magnets
Total Catch
Boat Operation
Boat Catch Records
Length Samples
Scale Samples
Egg and Larvae Samples
Hydrographic and Meteorological Data
CHARACTERISTICS OF CATCH
Total Catch
Intensity of Fishing
Length Composition

Figure 3. Conceptual model of how fishing affects the sardine resource (from Sette 1943).

among people and institutions with very different motives and objectives; it is a confederation that has productively endured for 40 years.

In 1949 the Marine Research Committee was established, and the CalCOFI program started; at that time it was called the California Cooperative Sardine Program. The technical committee—composed of scientists from the California Department of Fish and Game (CDFG), the U.S. Bureau of Commercial Fisheries (USBCF), the Scripps Institution of Oceanography (SIO), and the California Academy of Sciences (CAS)—laid out a rather ambitious program. The technical committee wrote that

> in order to develop plans for the responsible management of the sardine resource, and to attempt to derive workable methods of predicting where sardines will be found, and in what quantities, it is imperative to know certain underlying principles which govern the sardine's behavior, availability, and total abundance.

They further wrote that the four agencies participating in the program are

> investigating the sardine in relation to its physical and chemical environment, its food supply, its predators and its competitors, in attempting to evaluate the findings in terms of the survival of the young, and in terms of the distribution and availability of the sardines when they reach commercial size. (*California Cooperative Sardine Research Program Progress Report*, 1950)

This outline became known as the oceanographic approach to fisheries research. Essentially what the scientists wished to do was to correlate changes in water conditions with changes in sardine spawning, availability, and abundance. CAS researchers conducted laboratory studies on sardine behavior. CDFG staff monitored fishing effort and the size and age of the catch, as they had done since 1916. They also indexed recruitment from their bait-fishery surveys, collected adults for stomach analysis and reproductive condition, and conducted acoustic surveys for both juveniles and adults. SIO scientists estimated currents, correlated upwelling and wind fields, measured nutrient content, and—most important—developed new instruments for biological and oceanographic observations. USBCF researchers attempted to get the plankton sorted within one month, so as to adjust the survey scheme for changes in the spawning pattern of the sardines. Hopkins Marine Station joined in 1951; its researchers began weekly surveys of Monterey Bay.

The CalCOFI field sampling protocol is essentially a collection of plankton and water samples obtained over a fixed grid of stations (Figure 4) at periodic intervals. In the early days, other studies were made as well, although not as consistently. Phytoplankton tows were conducted; dip net fishing was done under night lights; and albatross and marine mammal counts were maintained. All three agencies acquired new research vessels to support the CalCOFI cruises. In 1954 the landing tax was extended to mackerel, anchovy, and herring. In 1955 the Marine Research Committee was expanded to include recreational fishermen and fishermen's unions.

The program was reviewed in 1957, 1961, and 1966. Each of these reviews resulted in a change in the sampling protocol. The cruises conducted in 1949 and 1950 were essentially exploratory surveys, and the sampling grid was fixed in 1951. Almost every month was sampled in every year throughout the 1950s (Figure 5). Twenty-five percent of the money spent on marine fisheries research in California was spent on the sardine, and half of that money was for vessel time. By 1955, approximately $4 million had been spent on sardine research. Of that, $800,000, or one-fifth, had been dispersed by the Marine Research Committee, with three-quarters going to SIO and USBCF.

By 1957 it was apparent that research directions among the three agencies had diverged, and a committee—John Marr from USBCF, John Radovitch from CDFG, John Isaacs from SIO, and Oscar Sette as a consultant—was formed to review the program. They suggested that a permanent coordinator be hired to provide some cohesiveness to the program, and that a permanent three-person committee, now known as the CalCOFI Committee, be established. They urged more data processing, analysis, and reporting.

By 1961 the CalCOFI Committee was in place, and Garth Murphy was the CalCOFI coordinator. The surveys had changed to quarterly, and covered larger areas, less frequently (Figure 6). By this time, it had been suggested that the anchovy was replacing the sardine, based on the assumption that they were ecological equivalents. It was widely acknowledged that several cold springs plus an intense fishery may have contributed to the sardine's decline.

The CalCOFI Committee stated that the sardine should not be studied as isolated from its ecological associates. The Committee wrote that "the sardine is like the gold of California—a conspicuous, valuable, easily harvested element in the midst of less-conspicuous riches of far greater potentiality."

The Committee also wrote that the "research should be responsible to the needs of society, and that the ultimate goal was to gain sufficient understanding to guide society in its use of natural resources."[2]

In 1966 the CalCOFI Committee decided that more thorough seasonal coverage was necessary to describe the spawning cycles of several species. Quarterly cruises every year were replaced with monthly or bimonthly cruises every three years (Figure 7). The Committee decided to document and study the developing anchovy fishery, which it had proposed a couple of years earlier, and secondly, to continue large-scale surveys of the California Current. Species of particular interest included hake, jack mackerel, and squid.

## EMERGENCE OF THE ANCHOVY

During this time, the northern anchovy emerged as a major coastal pelagic stock (Figure 8). In 1951, when the systematic surveys began, there were two sardine spawning centers—one off Cedros Island in southern Baja California, and another off northern Baja California and southern California. At this time, anchovy larvae and sardine larvae were equally abundant. By 1952 it was clear that the 1948 year class of the sardine was moderately strong, but that the 1949, 1950, and 1951 year classes were very poor—about one-sixth of the 1948 year class. The outlook of the fishery was "very bleak." By 1953, "very bleak" became catastrophic as the population contracted farther southward with a reduced age structure. In 1954 warm water appeared off California, sardines came north to spawn, and there were good catches along the coast. By this time, however, anchovy larvae had doubled in abundance, while sardines and Pacific mackerel continued to decline.

In 1955 Clark (CDFG) and Marr (USBCF)

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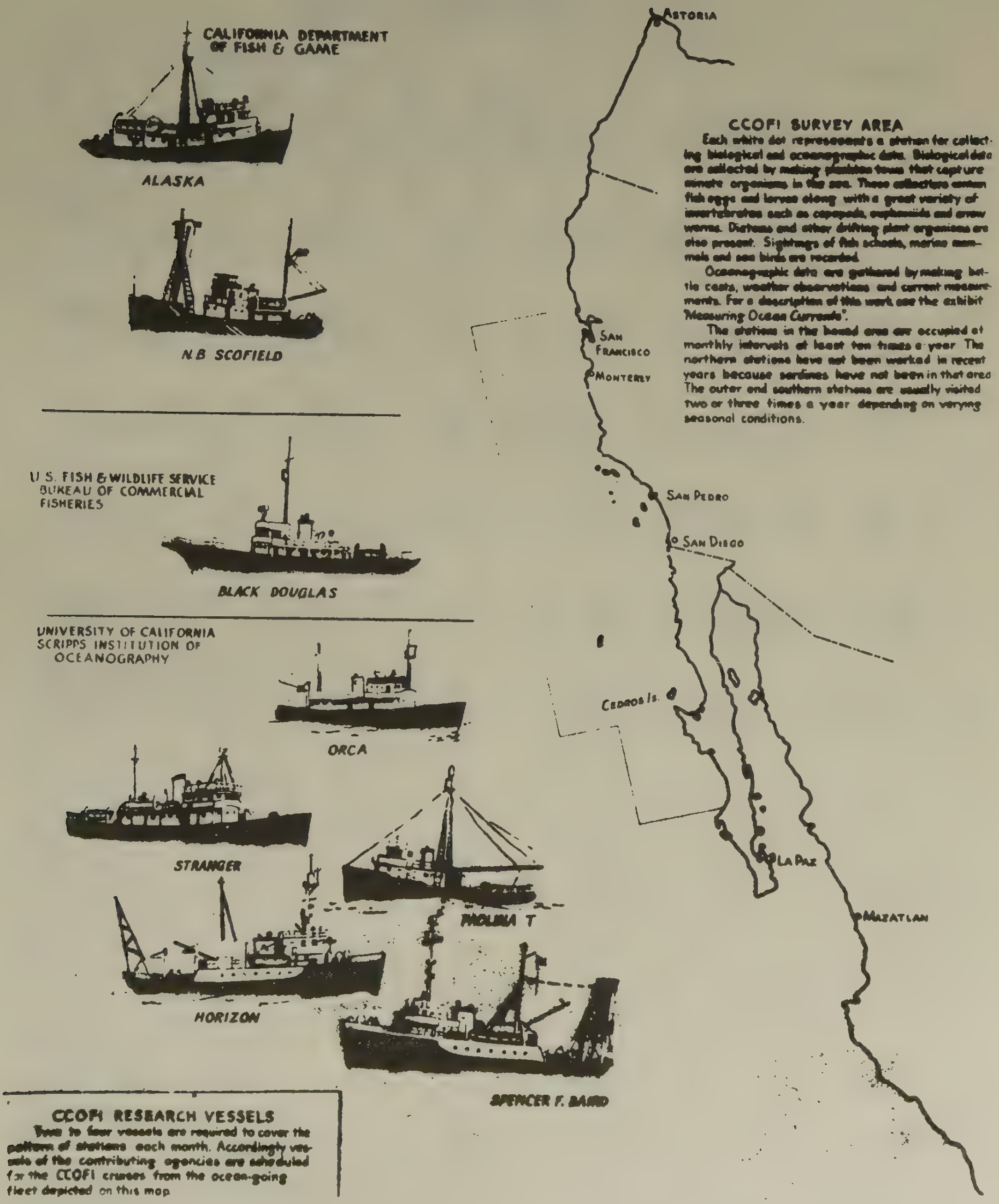
[2] *Calif. Coop. Oceanic Fish. Invest. Rep.* 8 (1961).


CALIFORNIA DEPARTMENT OF FISH & GAME
ALASKA
N.B SCOFIELD
U.S. FISH & WILDLIFE SERVICE BUREAU OF COMMERCIAL FISHERIES
BLACK DOUGLAS
UNIVERSITY OF CALIFORNIA SCRIPPS INSTITUTION OF OCEANOGRAPHY
ORCA
STRANGER
PAOLINA T
HORIZON
SPENCER F. BAIRD
ASTORIA
SAN FRANCISCO
MONTEREY
SAN PEDRO
SAN DIEGO
CEDROS Is.
LA PAZ
MAZATLAN

CCOFI SURVEY AREA

Each white dot represents a station for collecting biological and oceanographic data. Biological data are collected by making plankton tows that capture minute organisms in the sea. These collections contain fish eggs and larvae along with a great variety of invertebrates such as copepods, euphausiids and arrow worms. Diatoms and other drifting plant organisms are also present. Sightings of fish schools, marine mammals and sea birds are recorded.

Oceanographic data are gathered by making bottle casts, weather observations and current measurements. For a description of this work see the exhibit "Measuring Ocean Currents".

The stations in the boxed area are occupied at monthly intervals at least ten times a year. The northern stations have not been worked in recent years because sardines have not been in that area The outer and southern stations are usually visited two or three times a year depending on varying seasonal conditions.

CCOFI RESEARCH VESSELS

Two to four vessels are required to cover the pattern of stations each month. Accordingly vessels of the contributing agencies are scheduled for the CCOFI cruises from the ocean-going fleet depicted on this map.

Figure 4. CalCOFI station grid, from 1951 to present.

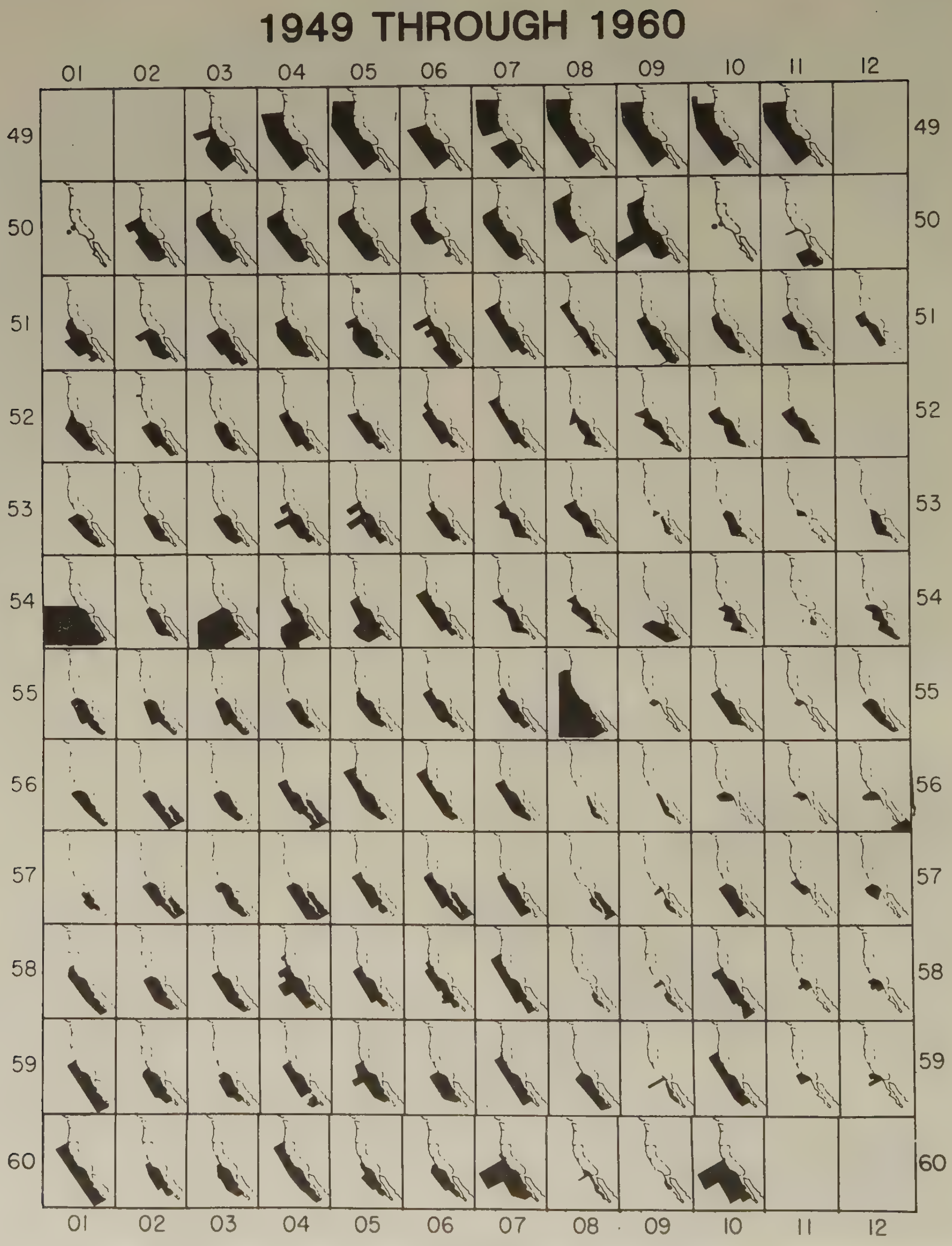

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Figure 5. CalCOFI cruises, 1949–60, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

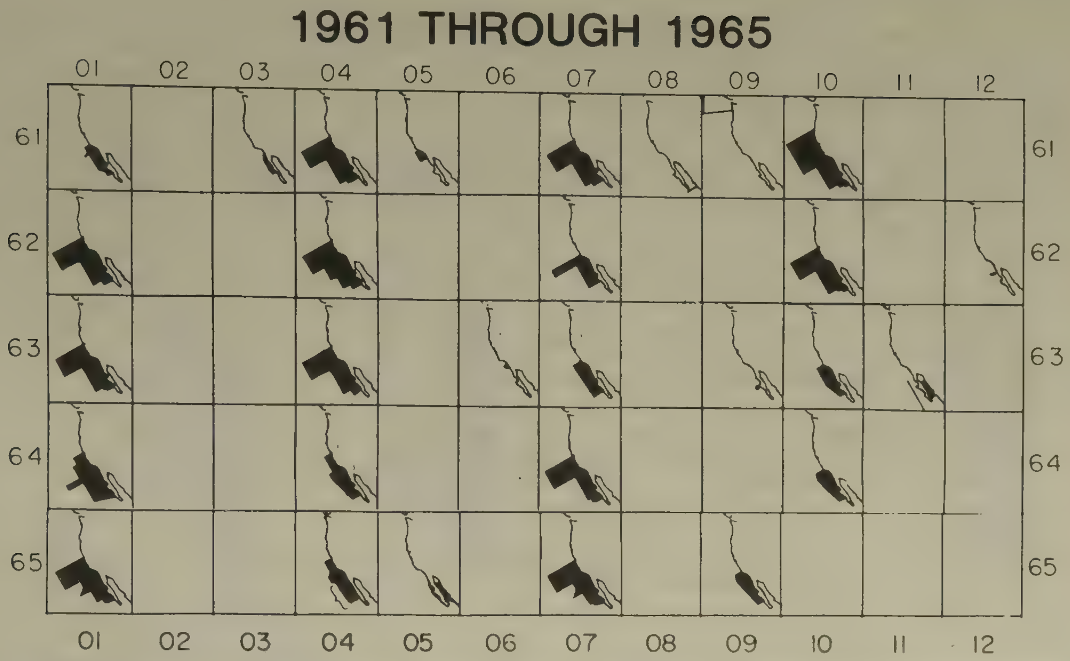

Figure 6. CalCOFI cruises, 1961–65, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

jointly published a paper in which they agreed to disagree on the population dynamics of the sardine. The disagreement was essentially whether or not a relationship existed between sardine spawning stock size and recruitment—that is year-class strength. The arguments implied that either overfishing (Clark) or an adverse environment (Marr) caused the decline in sardine population. 1957 and 1958 brought another warm period, and the sardines spawned as far north as Monterey. There were good catches all along the coast.

In the late 1950s a picture began to emerge. Sardines spawning off southern California were thought to migrate north to Oregon and Washington; sardines spawning off Baja California were thought to migrate to northern California. The lack of spawning success off southern California since 1943 was probably the cause of the collapse of the northern fisheries. Poor spawning success was further thought to be due to low spring temperatures. In 1958, Reid, Roden, and Wyllie published their paper on the physics of the California Current. They suggested that increased winds, enhanced upwelling, and cooler temperatures may have been associated with spawning failures. Later that year CalCOFI sponsored a symposium on the changing Pacific Ocean, and most participants agreed that 1957 had terminated a monotonous decade of low temperatures and high winds in the North Pacific.

By the early 1960s, there was a general acknowledgement that overfishing for sardines had occurred, and the anchovy-sardine replacement hypothesis began to receive some interest. Both Isaacs (1965) and Ahlstrom (1967) published papers on the strong association between anchovy larvae and sardine larvae. By 1958 and 1959, anchovy larvae were three times as abundant as they had been in 1951, and they doubled again in the early 1960s. The anchovy-to-sardine ratio was 3 to one in 1952. By 1956, it was 10 to one; by 1959, 45 to one; and by 1962 there were 80 anchovy larvae for every sardine larva. The suggestion was made at that time that anchovy and sardine may together act as a single population, and that a large sardine-anchovy population may depress year-class strength.

In 1964 the CalCOFI Committee proposed an experimental anchovy fishery. They suggested annual harvests of 200,000 tons of anchovy and

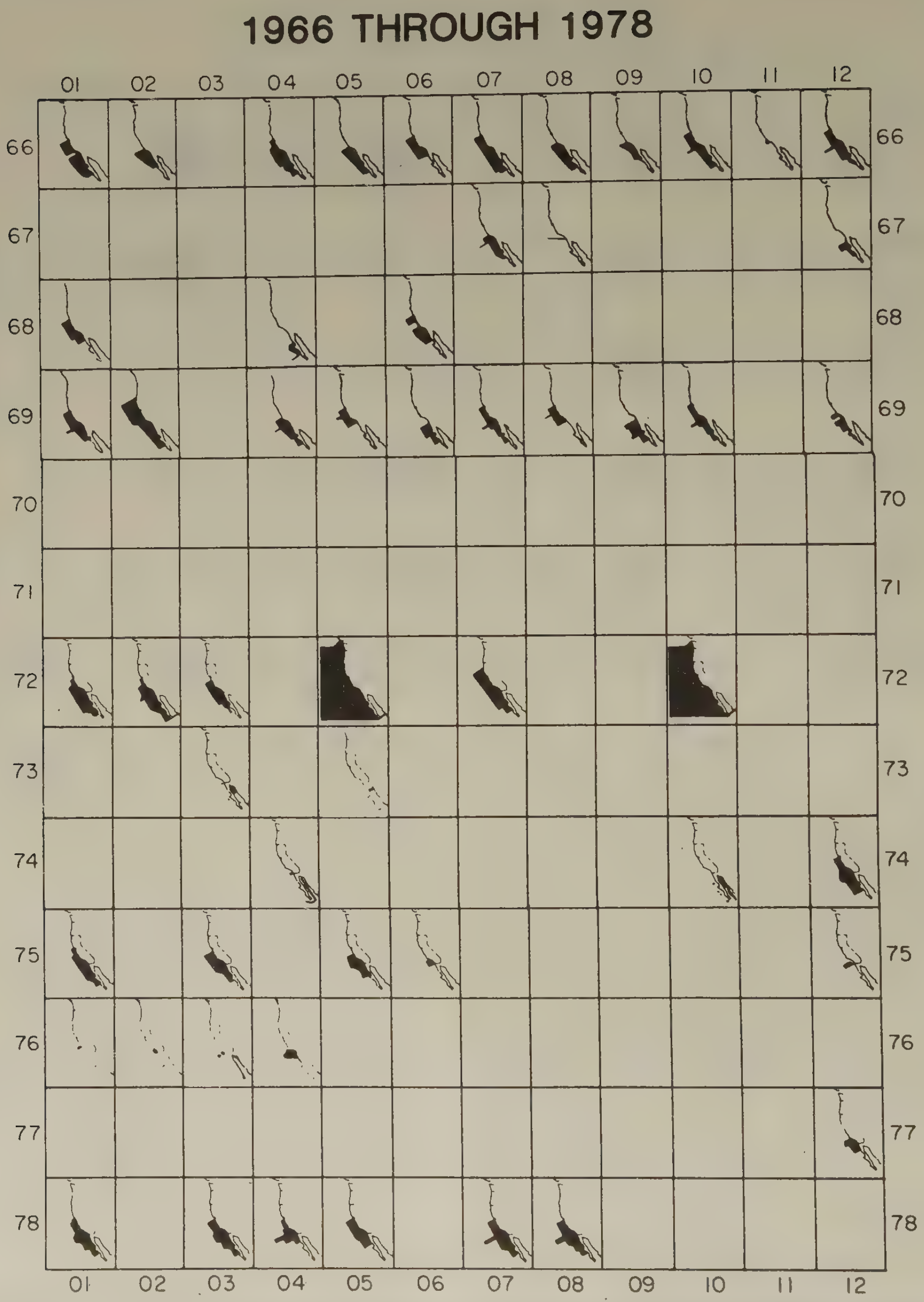
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Figure 7. CalCOFI cruises, 1966–78, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

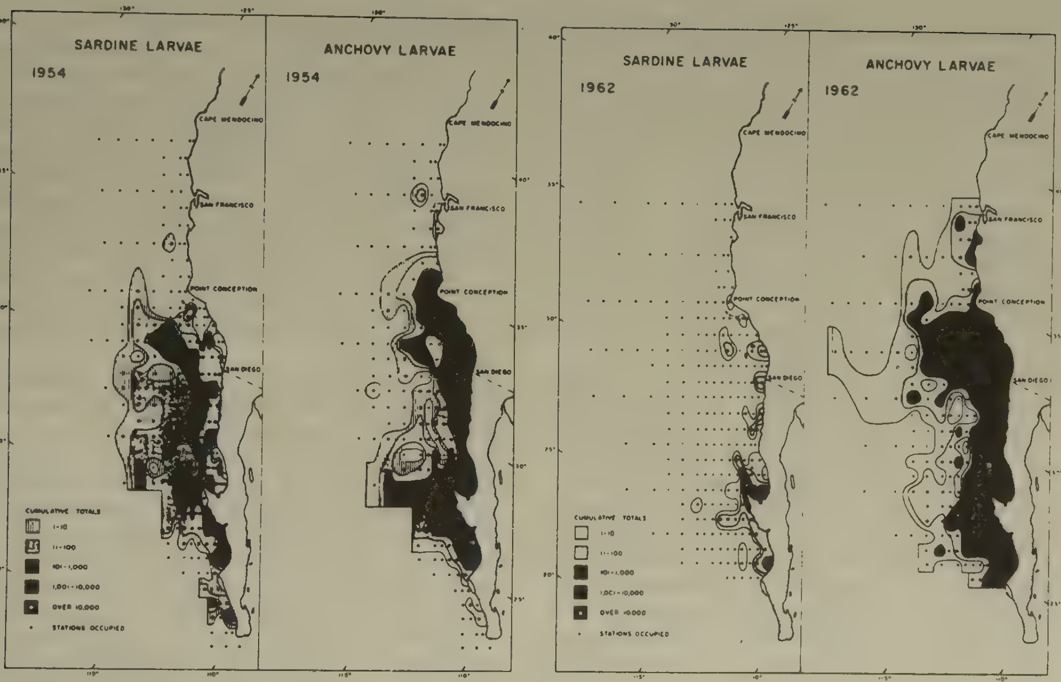

Figure 8. Distributions of sardine and anchovy larvae, 1954 and 1962 (from Ahlstrom 1966).

10,000 tons of sardines. These catches would be sufficient to reduce the anchovy biomass, and still monitor the sardine response. There was a strong negative reaction across the state, and the experiment never got off the ground.

Instead the CalCOFI Committee decided to continue work on the sardine-anchovy relationship, as well as to expand broadscale studies of the pelagic environment. Attention was directed toward other species such as saury, hake, jack mackerel, and squid. The Marine Life Research Program at Scripps expanded its studies into the North Pacific, and Joe Reid convened the 1966 CalCOFI symposium on wide-scale studies of the Pacific Ocean.

In the late 1960s the CalCOFI Committee was frustrated that the anchovy fishery had failed to develop, and they proposed research to identify factors that constrained the use of living marine resources in California. In 1967 CalCOFI sponsored a symposium on the magnitude, distribution, and susceptibility of living marine resources in the California Current. In 1968 the CalCOFI symposium covered the legal, sociological, and technical problems associated with the use of marine resources in the state of California. The 1969 symposium was on world population growth and the role of marine fisheries in providing food. The CalCOFI Committee wrote that there was an understanding of pelagic resources in the California Current sufficiently adequate for the scientific management of multiuse domestic fisheries, and yet the resources remained little used.

The committee suggested two reasons for this: the first was a general failure to appreciate the long-term economic benefits of a healthy domestic fishing industry; the second was misunderstanding and mistrust between users of the resource—essentially, a widespread apprehension that the state could not control a fishery once it got started. This fear was not groundless, given the sardine experience.

## EXPORT OF TECHNOLOGY

By the 1970s, however, CalCOFI began to turn outward. In the 1950s, we were concerned about the decline of the sardine. In the 1960s we were concerned about the increase of the anchovy. In the 1970s, we were concerned about exporting what we knew. CalCOFI became an international model for the study of pelagic populations and the large-scale oceanographic and meteorological events that affect them. USBCF became part of NOAA, an agency with a strong tradition of environmental mapping and monitoring. The MARMAP program was established to assess pelagic stocks off the eastern and gulf coasts; it was modeled after CalCOFI. The CalCOFI Committee established a relationship with Instituto Nacional de Pesca in Mexico, and eventually a Mexican anchovy fishery developed. The Sardine Anchovy Recruitment Program (SARP) is also an example of the worldwide influence of CalCOFI ideas.

In 1979 the Marine Research Committee was retired, and an abbreviated CalCOFI program continued by agreement between the state and federal agencies. Surveys and ship time were reduced to what was necessary to monitor certain populations (Figure 9), and a search was made for "indicator stations," that is, stations that could be routinely sampled to represent a much larger survey. By this time, the Marine Research Committee had distributed $3.5 million over its 30-year existence. A little less than $1 million of that came from the sardine, $1.2 million from the anchovy, $1 million from the mackerels, and $⅓ million from squid and herring.

CalCOFI continued as a forum to bring researchers together to collaborate and present results. *CalCOFI Reports*, published once a year, became a peer-reviewed journal. The CalCOFI Committee sponsored symposiums on nonconsumable resources in the California Current, climatic regimes and low-frequency events, mesoscale patterns and processes, eastern boundary currents as a class of phenomena, and nearshore patterns and processes. The goals were restated: to understand the physical and chemical environment and how it changes, to determine the productivity of the California Current ecosystem, and to make this information available in the form of *CalCOFI Reports*, conferences like this one, and data bases. The ultimate goal is still to understand and predict fluctuations in marine populations and to provide a basis for the wise use of these resources.

## EGG PRODUCTION SURVEYS

We have changed some of our methods as well. In 1972 Paul Smith gave us a way to determine absolute abundance from ichthyoplankton surveys when he regressed larval census on Murphy's population estimates of the sardine. In this formulation, the numbers of larvae found in the sea are thought to be proportional to the adult spawning biomass. This assumes two things: (1) that every year there is a constant reproductive output per unit weight of adult, and (2) that the mortality of the young is constant from year to year. This technique became known as the larval census method.

The larval census method eventually evolved into the egg production method (Lasker 1985), by which the spawning biomass is proposed to be the quotient of the daily production of eggs in the sea and the daily specific fecundity of the adults. This method directly measures both the reproductive output of adults and the mortality of the young. The only assumption required is that we can sample without bias.

Reproductive output of adults is determined from a sample of adult fish. Various reproductive parameters are measured and combined to estimate the daily specific fecundity—the number of eggs spawned per day per unit weight of adult fish.

Egg production, the number of eggs spawned per day, is determined from high-density surveys conducted over the spawning habitat. Each of these surveys (Figure 10) comprises approximately 1,000 vertical egg tows yielding a rather precise estimate of egg abundance by developmental stage, from which we can determine egg production. These surveys are also part of the CalCOFI data base.

## CALCOFI ON-LINE DATA SYSEM

CalCOFI data are available in a variety of hardcopy reports and papers. There are approximately 300 data reports, 30 atlases, and 29 volumes of *CalCOFI Reports*. In addition, at the Southwest Fisheries Center we have developed a computerized data search-and-retrieval system called the CalCOFI On-Line Data System. It is intended to give researchers the opportunity to explore the extent of the CalCOFI data set and to extract desired portions. Although it does not provide access to every CalCOFI data set, the major portion of the CalCOFI data (ichthyoplankton counts and hydrocast profiles) is available in this initial version.

The researcher is guided through the system by a series of menus (Figure 11). The main menu offers four options: (1) station index, (2) methodology, (3) ichthyoplankton data, and (4) hydrocast data. The station index option allows a researcher to peruse the extent of the data, providing access to information on the various cruises, the geographic sampling density (the extent of the area sampled during a particular cruise), and the temporal sampling density (how often a specific area was sampled throughout the time series). The

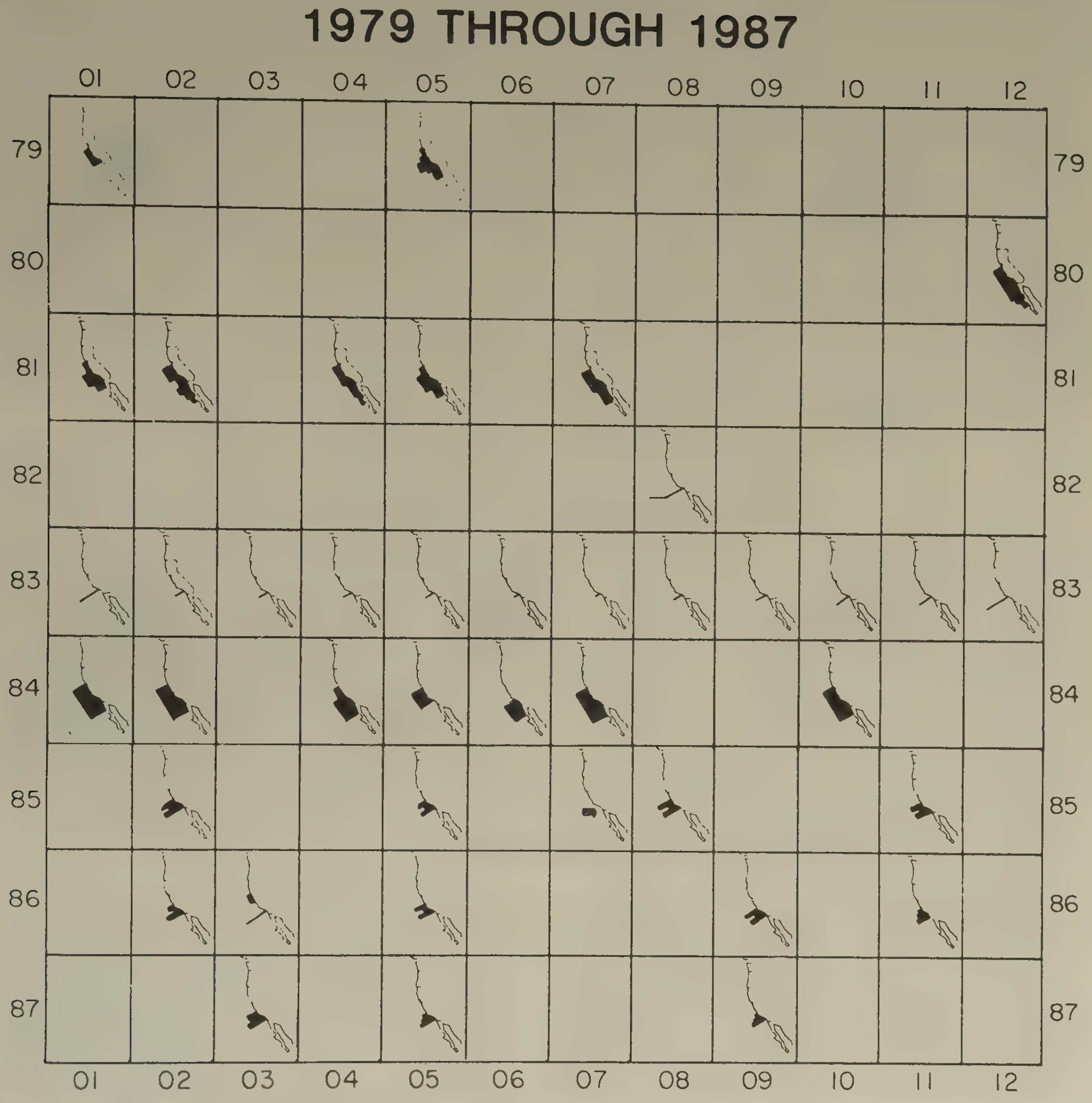

Figure 9. CalCOFI cruises, 1979–87, based on information compiled by A. Mantyla at Scripps Institution of Oceanography. Shaded areas indicate geographic extent of cruises.

methodology option allows a researcher to peruse descriptions of the data sets currently on line, cruise frequency and geographic coverage, gear design, sample sorting and archiving procedures, identification notes, and annotated references. The ichthyoplankton data option allows a researcher to actually extract data. Data are available on five major species of fish larvae enumerated by length, anchovy eggs enumerated by developmental stage, and the extensive collection of fish eggs and fish larvae identified to over 200 taxonomic categories. The hydrocast data option allows access to a data set of vertical profiles of temperature, salinity, oxygen, oxygen saturation,

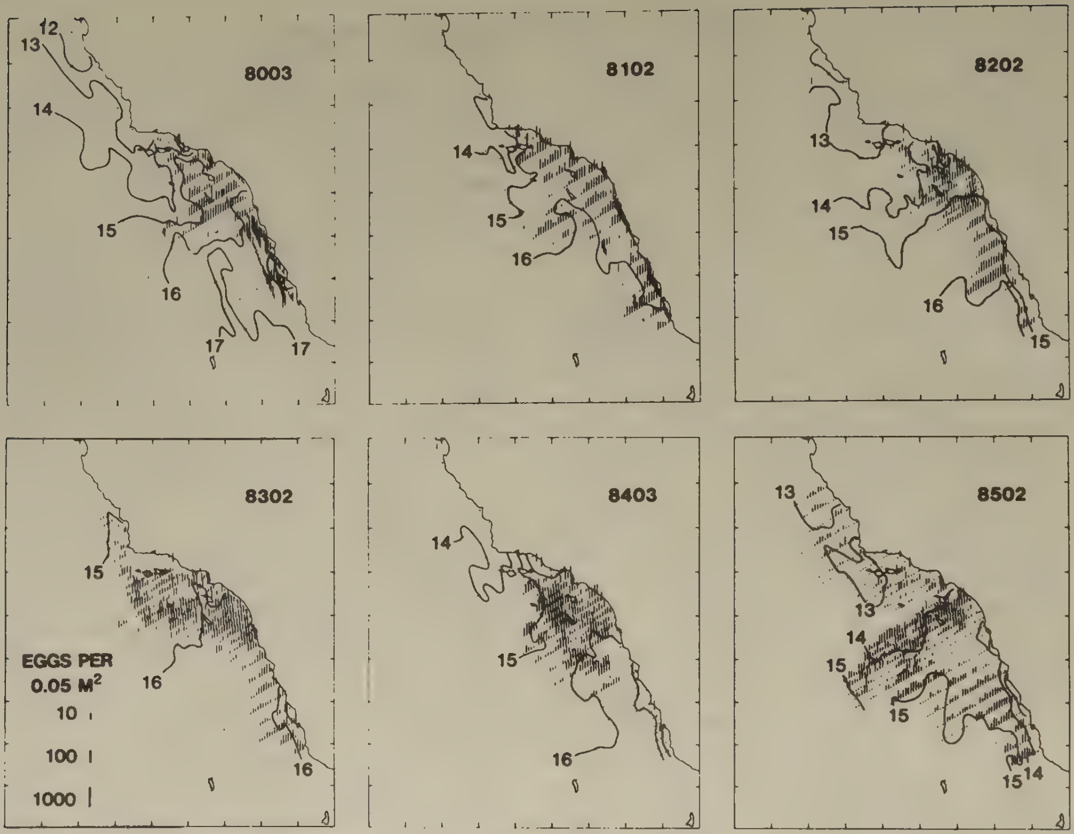

Figure 10. Northern anchovy egg production surveys, 1980–85 (from Fiedler et al. 1986).

density, and dynamic height determined at standard depths.

The data are the results of approximately 300 survey cruises during which 50,000 plankton tows and 10,000 hydrocasts were conducted. The data are displayed on a terminal screen in the form of tables and maps; they can also be written to a computer file for subsequent analysis or printing.[3]

## LARGE-SCALE SURVEYS

I close by listing three reasons for conducting large-scale surveys and building a long-term time series like CalCOFI: (1) to determine what species reproduce when and where, what their distribution is, and something about how they recruit themselves—where survival is high and where it is low; (2) to characterize physical habitats, their seasonal and interannual change; and (3) to monitor long-term population trends and variability. These were the intentions of the first CalCOFI surveys, and I believe that they are still valid. Consideration should be given, however, to updating the sampling schemes and the tools that we use.

* * *

**Question:** Are the Gulf of California data in the CalCOFI On-Line Data System?

**Hewitt:** Not at the present time. That doesn't mean that the data can't be added later, but they are not there now. The Gulf of California cruises were

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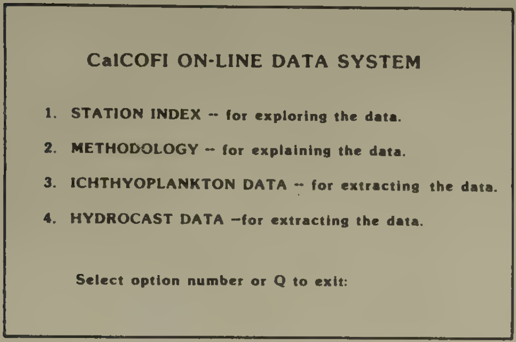
[3] User's manuals for the CalCOFI On-Line Data System may be obtained from the Southwest Fisheries Center, P.O. Box 271, La Jolla CA 92038.



```
            CalCOFI ON-LINE DATA SYSTEM

  1. STATION INDEX -- for exploring the data.

  2. METHODOLOGY -- for explaining the data.

  3. ICHTHYOPLANKTON DATA -- for extracting the data.

  4. HYDROCAST DATA --for extracting the data.


     Select option number or Q to exit:
```

Figure 11. Main menu from the CalCOFI On-Line Data System (from Hewitt et al. 1988).

rather sporadic and don't constitute a continuous time series.

**Dick Schwartzlose:** One of the many things I would like to say, having been in CalCOFI for many years and having been in the administration of the Marine Life Research Program at Scripps for those many years also, is that you notice changes in the cruise frequency from almost every month to every quarter. A lot of people criticized the change and said that we should have continued the monthly cruises. Of course that would have been very nice to do, but at the time all of the agencies were coming under financial stress, and it was impossible to continue the ship operations at a high level, and also to supply the number of people necessary to go on all those cruises. The decision to shift the cruises to a quarterly frequency was not made just because we thought we didn't need them. There was also a consideration of what finances were available. This occurred again in the 1970s as more money and people were diverted to process-oriented cruises, and so there were other ships in the pattern of cruises. Since that time CalCOFI has been criticized for not continuing the monthly cruises. But of course we can't peer into the future to see what's best and what's going to happen.

**Hewitt:** One of the things that I hoped would come out today is a more rational discussion of what should be measured, how often, over how large an area, using what tools, and so forth. It would be based on a more rational approach to the problem at hand rather than an irrational response to budget restrictions.

**Paul Smith:** I think it should be pointed out that in 1957, when the Russians launched the Sputnik, the government of the United States launched a series of expenditures on oceanography which tended to double every year from 1957 to 1965. It was during this same period that the CalCOFI surveys were reduced to quarterly. So instead of a reduction in the absolute availability of funds, there was a reduction of the will to conduct the work. Individuals were awarded funds and carried out the work under the names of spin-off organizations. The money was carried away, as were a lot of the people at that time. So I don't think it was the shortage of funds; rather it was a shortage of will.

## LITERATURE CITED

Ahlstrom, E. H. 1966. *Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951–64: a summary.* U.S. Fish and Wild. Serv. Spec. Sci. Rep. 534, 71 pp.

———. 1967. Co-occurrences of sardine and anchovy larvae in the California Current region off California and Baja California. *Calif. Coop. Oceanic Fish. Invest. Rep.* 11:117–135

Clark, F. N., and J. C. Marr. 1955. Population dynamics of the Pacific sardine. *Calif. Coop. Oceanic Fish. Invest. Rep.* 4:11–48.

Fiedler, P. C., R. D. Methot, and R. P. Hewitt. 1986. Effects of California El Niño 1982–1984 on the northern anchovy. *J. Mar Res.* 44:317–338.

Hewitt, R. P., S. Jacobson, and C. Meyer. 1988. *CalCOFI On-Line Data System, programmer's manual, version 1.0.* SWFC Admin. Rep. LJ-88-03, 120 pp.

Isaacs, J. D. 1965. Larval sardine and anchovy interrelationships. *Calif. Coop. Oceanic Fish. Invest. Rep.* 10:102–140.

Lasker, R., ed. 1985. *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy,* Engraulis mordax. NOAA Tech. Rep. NMFS 36, 99 pp.

McEvoy, A. F. 1986. *The fisherman's problem: ecology and law in the California fisheries 1850–1980.* Cambridge and New York: Cambridge Univ. Press, 368 pp.

Reid, J. L., Jr., G. I. Roden, and J. G. Wyllie. 1958. Studies of the California Current system. *Calif. Coop. Oceanic Fish. Invest. Rep.* 6:28–56.

Sette, O. E. 1943. *Structure of a research program to determine how fishing affects the resource.* U.S. Fish Wild. Serv. Spec. Sci. Rep. 19; also reissued in 1950 as part of U.S. Fish Wild. Serv. Spec. Sci. Rep. 15.

Smith, P. E. 1972. The increase in spawning biomass of the northern anchovy, *Engraulis mordax. U.S. Fish Bull.* 70 (3):849–874

Steinbeck, J. 1954. *Sweet thursday.* New York: Viking Press.

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# STATUS OF THE TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, FISHERY OFF SOUTH CAROLINA AND GEORGIA AND RECOMMENDATIONS FOR MANAGEMENT

JOSEPH E. HIGHTOWER[1] AND GARY D. GROSSMAN[2]

## ABSTRACT

We used a sex- and age-structured model and CPUE data from commercial and research vessels to assess the current status of the tilefish, *Lopholatilus chamaeleonticeps*, substock off South Carolina and Georgia. Based on commercial CPUE data and assumed natural mortality ($M$) rates of 0.10–0.25, we estimated that adult population density prior to fishing ranged from 603 to 950 per km$^2$ and stock biomass ranged from 1,130 to 1,570 tonnes (t). Our estimates of the recommended fishing mortality rate ranged from 0.10 ($M$ = 0.10) to 0.48 ($M$ = 0.25), resulting in sustainable yields of 40 ($M$ = 0.10) to 82 t ($M$ = 0.25) per year. We obtained higher estimates of virgin population density (883–1,710 per km$^2$) when research CPUE data were used. Sustained yield estimates also were higher, ranging from 55 ($M$ = 0.10) to 148 t ($M$ = 0.25) per year. Average estimates of recommended yield from commercial and research CPUE data were 58 and 95 t, respectively. Observed yields in the developing fishery exceeded 100 t in 1981–84 and in 1986; however, current observations indicate that fishing effort has declined to a low level in response to reduced catches. Based on the assumption that commercial CPUE data better reflect population trends, we recommend that the annual harvest not exceed about 50 t, which should result in a stock biomass of about 400–800 t. Apparent limitations on sustainable yield from the fishery probably can be attributed to the long lifespan, slow growth rate, and sedentary nature of tilefish.

The tilefish, *Lopholatilus chamaeleonticeps*, is a large demersal species found along the outer continental shelf of North America from Nova Scotia to Key West, FL, along the Gulf coast to Campeche Bank, and off South America from Venezuela to Surinam (Freeman and Turner 1977). Tilefish are long-lived and have relatively slow growth rates (Harris and Grossman 1985). They are most common at depths of 100–400 m and water temperatures of about 9°–14°C (Freeman and Turner 1977). Abundance is greatest in areas where substrates are suitable for burrow construction (Able et al. 1982; Grossman et al. 1985) or afford other shelter such as scour depressions around boulders (Valentine et al. 1980) or rubble piles (Low and Ulrich 1983).

Katz et al. (1983) described two genetically distinct tilefish stocks through use of morphometric and electrophoretic data: one composed of tilefish from the Middle Atlantic Bight (MAB), and one composed of tilefish from the South Atlantic Bight (SAB) and Gulf of Mexico. Larval transport from the Gulf of Mexico to the SAB may be responsible for similarities in electrophoretic results for these two areas (Katz et al. 1983). Katz et al. (1983) suggested, however, that it may be necessary to manage these substocks separately because of their wide geographic separation. If true, this should be done with the understanding that Gulf of Mexico populations may serve as a source of recruits to SAB populations (Katz et al. 1983).

Tilefish have been harvested commercially in the MAB since 1915, with annual landings ranging from <1 tonne (t) to 4,500 t (Turner et al. 1983). Landings from the SAB and Gulf of Mexico were small prior to 1980 (Low et al. 1983). A limited number of tilefish were caught incidentally in the deepwater grouper fishery off South Carolina (Low and Ulrich 1982). Recreational catches were small because of the depth at which tilefish occur (Low and Ulrich 1982). Commercial fisheries have since developed in both the SAB and Gulf of Mexico, due in part to an interest in diversification within the shrimp industry (Low et al. 1983).

For the segment of the SAB tilefish fishery operating off South Carolina and Georgia, increased fishing effort has resulted in a substantial increase in tilefish landings since 1978 (Table 1). In addition, a considerable number of tilefish caught off Georgia

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TABLE 1.—South Carolina and Georgia tilefish, *Lopholatilus chamaeleonticeps*, landings from 1978 to 1986. Georgia landings of tilefish and blueline tilefish, *Caulolatilus microps*, were not reported separately routinely prior to 1985. Landings by gear type were available for 1980–85, however, so rod and reel and electric reel catches of unclassified tilefish (which are almost exclusively blueline tilefish) were excluded to yield a more accurate estimate of Georgia tilefish landings.

| | Landings (metric tons) | | |
|---|---|---|---|
| Year | South Carolina[1] | Georgia[2] | Total |
| 1978 | 2.59 | [3]0.10 | 2.69 |
| 1979 | 10.08 | [3]0.02 | 10.10 |
| 1980 | 43.89 | (confidential) | >43.89 |
| 1981 | 103.74 | 0.35 | 104.09 |
| 1982 | 163.78 | 7.99 | 171.77 |
| 1983 | 252.55 | 6.67 | 259.22 |
| 1984 | 190.44 | 39.49 | 229.93 |
| 1985 | 70.49 | 13.04 | 83.53 |
| 1986 | 142.96 | (confidential) | >142.96 |

[1] Andy Jennings, Fisheries Statistics Office, South Carolina Wildlife and Marine Resources Department, Charleston SC, pers. commun. 1987.

[2] S. Gordon Rogers, Fisheries Statistics Coordinator, Georgia Department of Natural Resources, Brunswick, GA, pers. commun. August 1987.

[3] Georgia Department of Natural Resources. 1983. Georgia landings annual summary 1980. Ga. Dep. Nat. Resour., Coastal Resour. Div., Brunswick, GA.

from about 1982 to 1984 were landed in Florida; therefore, landings in Table 1 are a conservative estimate of removals from these grounds.

Low et al. (1983) provided a preliminary estimate of maximum sustained yield (MSY = 162 t) for the developing fishery. Their estimate was derived from Gulland's (1971) model MSY $= 0.5MB_0$, where $M$ was the natural mortality rate and $B_0$ was an estimate of virgin biomass. Our objective was to provide updated yield estimates for use in managing the tilefish fishery off South Carolina and Georgia. We base these estimates on the 9-yr sequence of catches from the developing fishery as well as recently obtained information on the growth, mortality, and reproductive biology of tilefish from this area.

## METHODS

We used a deterministic sex- and age-structured model to simulate the developing tilefish fishery and to calculate sustainable yields. The model was based on the following assumptions and data sources. We assumed that the natural mortality rate ($M$) ranged from 0.10 to 0.25 (Harris and Grossman 1985). We used sex-specific estimates of weight-at-age because the von Bertalanffy growth curves and length-weight relationships used to calculate weight-at-age differed significantly by sex (Harris and Grossman 1985). We used maturity-at-length data (Erickson and Grossman 1986) to estimate maturity at age by using a logistic model:

$$p_{s,a} = 1/(1 + \exp(-b_{Mat}(L_{s,a} - L50_{Mat}))) \qquad (1)$$

where $p_{s,a}$ was the proportion of sex-$s$, age-$a$ fish that were sexually mature, $b_{Mat}$ was a parameter affecting the steepness of the curve, $L_{s,a}$ was the standard length (SL) of sex-$s$ fish at age $a$, and $L50_{Mat}$ was a parameter representing the length at which 50% of the fish were sexually mature. We assumed that the total biomass of sexually mature females ($S_f$) was an adequate measure of spawning potential.

We used a logistic model to relate selectivity to length:

$$sel_{s,a} = 1/(1 + \exp(-b_{Sel}(L_{s,a} - L50_{Sel}))) \qquad (2)$$

where $sel_{s,a}$ was the proportion of sex-$s$, age-$a$ fish that were vulnerable to fishing, $b_{Sel}$ was a parameter affecting the steepness of the curve, and $L50_{Sel}$ was a parameter representing the length at which 50% of the fish were vulnerable to fishing. Based on length-frequency data (Harris and Grossman 1985), we assumed that female and male tilefish reached 50% vulnerability at about 475–500 and 500–525 mm SL, respectively. We used a slope parameter ($b_{Sel}$) of 0.05 so that selectivity-at-age in the simulated fishery ranged from about 0 at age 5 to 1.0 at age 11 (Harris and Grossman 1985). Parameter estimates used in the model are summarized in Table 2.

We assumed that the relationship between spawning stock size and subsequent recruitment was weak or nonexistent because 1) tilefish produce pelagic larvae (Fahay and Berrien 1981); 2) there may be substantial egg or larval transport between the Gulf of Mexico and SAB (Katz et al. 1983); and 3) tilefish are dependent on the availability of shelter (Valentine et al. 1980; Able et al. 1982; Low and Ulrich 1983; Grossman et al. 1985). To represent the stock-recruitment relationship, we used a Beverton-Holt curve of the following form (Kimura 1988):

$$N_{s,6}[t + 6] = \frac{0.5N_6[0]S_f[t]/S_f[0]}{1 - \mathrm{A}(1 - S_f[t]/S_f[0])} \qquad (3)$$

where $N_{s,6}[t + 6]$ was the number of sex-$s$, age-6 recruits in year $t$ + 6, $N_6[0]$ was the virgin recruitment level for both sexes combined, and $S_f[t]$ and $S_f[0]$ were the biomass levels for spawning females in year $t$ and prior to fishing, respectively. The parameter A controlled the degree of density-dependence. We assumed that recruitment was either constant (A = 1.000) or decreasing by 10% when the spawning stock was reduced by 50% (A = 0.889). Few studies have shown a statistically significant relationship between spawning stock and recruitment (Hennemuth 1979); nevertheless, recruitment would be expected to decline at high *F*s. For that reason, we used the latter assumption to explore the effect of the stock-recruitment relationship on the form of the yield curve. Other investigators have used this approach to obtain conservative estimates of equilibrium yield when information on the stock-recruitment relationship was unavailable (Lenarz and Hightower 1985; Henry 1986; Hightower and Lenarz 1986).

We simulated the fishery using virgin recruitment levels of 10,000–200,000 6-yr-old fish. This range would result in virgin population sizes of 45,000–2.1 million fish, depending on the assumed level of natural mortality. Assuming that the area inhabitated by tilefish off South Carolina and Georgia is about 476 km$^2$ (Low et al. 1983), these population sizes correspond to adult densities of 95–4,400 per km$^2$. This appeared to be an adequate range of densities, given that estimates of tilefish burrow density in the Hudson and Veatch Canyons off southern New England ranged from 119 to 2,434 per km$^2$ in 1980 (Grimes et al. 1986). As Low et al. (1983) noted, the 1974–78 catch rates off southern New England (0.49–0.93 kg/hook; Grimes et al. 1980) were similar to the 1981–82 catch rate in the expanding fishery off South Carolina and Georgia (0.86 kg/hook).

TABLE 2.—Parameter estimates for the sex- and age-structured model of the tilefish fishery off South Carolina and Georgia.

| | Female | Male |
|---|---|---|
| von Bertalanffy[1] | | |
| $L_\infty$ | [2]792 | 922 |
| $k$ | 0.090 | 0.086 |
| $t$(zero) | −1.774 | −0.920 |
| Length-weight[1] | | |
| $b(1)$ | 2.28572E-8 | 7.92693E-9 |
| $b(2)$ | 2.974 | 3.141 |
| Maturity-at-age | | |
| $b_{Mat}$ | 0.030 | 0.018 |
| $L50_{Mat}$ | 495 | 458 |
| Selectivity-at-age | | |
| $b_{Sel}$ | 0.05 | 0.05 |
| $L50_{Sel}$ | 475, 500 | 500, 525 |

[1] Harris and Grossman (1985). Length-weight relationship: $w = b(1)L^{b(2)}$.

[2] The estimate of $L_\infty$ in Harris and Grossman (1985) (895 mm) was incorrect.

Because tilefish catches were negligible prior to 1978, the starting (1978) number-at-age vector at each recruitment level was assumed to be the equilibrium vector obtained at an *F* of 0. We assumed that our estimates of total landings were much more reliable than our estimates of fishing effort. For that reason, we solved iteratively for the sequence of fishing mortality rates that would produce the observed 1978–86 catches (Methot in press). For example, we began by solving for the 1978 *F* that would produce the 1978 catch biomass, and then used that *F* to project the number-at-age vector remaining in 1979. [We assumed that the final (1986) *F* should not exceed 2.0 (an exploitation rate of 80–84%), in order to rule out those cases where the 1986 harvest was attained by removing essentially all remaining tilefish.] Using this approach to estimate *F*, the observed and simulated catch biomass levels match exactly, although the observed and simulated age distributions may be different. Note that if we had a similar degree of confidence in our estimates of catch and fishing effort, it might be more appropriate to minimize differences between observed levels and model estimates of both catch and effort (see for example, Deriso et al. 1983), rather than forcing the model to reproduce the catches exactly.

At each virgin recruitment level, we calculated the correlation between the estimated 1978–86 *F*s and estimates of total effort based on CPUE data. We used two sources of CPUE data: 1) commercial snapper reel CPUE from 1980 to 1982 South Carolina vessels (Low and Ulrich 1983); and 2) mean longline CPUE from 1982 to 1985 research cruises aboard the RV *Georgia Bulldog*. Based on commercial snapper reel kg/landing (figure 13 in Low and Ulrich 1983), we estimated that observed annual landings would have required more than 22 trips in 1980, 89 in 1981, and 445 in 1982 (Table 3). Using research cruise estimates of longline kg/hook, we estimated that observed annual landings would have required 351,000 hooks fished in 1982, 1.9 million in 1983, 1.6 million in 1984, and 380,000 in 1985 (Table 3). The research catches were made using standard commercial longline gear (Harris and Grossman 1985). We also obtained a composite 1980–85 effort series using the ratio of hooks fished to trips in 1982 (Table 3), but our results were the same as when only research CPUE data were used.

At each level of natural mortality, we selected the virgin recruitment level that maximized the correlation between estimates of *F* and fishing effort. The selected recruitment level was used in the equilib-

TABLE 3.—Estimates of total effort based on commercial and research catch per unit effort (CPUE) and total commercial landings. Estimates of 1980–82 commercial CPUE (kg/landing) were based on landings by snapper reel vessels (figure 13, Low and Ulrich 1983). Research CPUE estimates (kg/hook) were based on longline sets aboard the RV *Georgia Bulldog*; each estimate is an average of seasonal averages from spring, summer, and fall cruises. Estimates of hooks fished in 1980 and 1981 were based on the commercial CPUE data, using the ratio of trips to hooks fished in 1982.

| Year | CPUE Commercial (kg/landing) | CPUE Research (kg/hook) | Total landings (kg) | Estimated trips | Estimated hooks fished |
|---|---|---|---|---|---|
| 1980 | 1,950 | — | >43,890 | >22 | (>17,331) |
| 1981 | 1,174 | — | 104,090 | 89 | (70,110) |
| 1982 | 386 | 0.490 | 171,770 | 445 | 350,551 |
| 1983 | — | 0.137 | 259,220 | | 1,892,117 |
| 1984 | — | 0.140 | 229,930 | | 1,642,357 |
| 1985 | — | 0.220 | 83,530 | | 379,682 |

rium yield calculations. Our approach for selecting virgin recruitment levels was based on the "tuning" process used in cohort analysis (Mohn 1983; Rivard 1983). In that approach, auxiliary information is used to "adjust" or "fine-tune" the estimates iteratively so that the output from cohort analysis "matches" some series of observations (Rivard 1983). The level of agreement between the observations and model predictions can be measured using correlation or regression techniques (Mohn 1983).

We obtained estimates of equilibrium yield by expressing the number of sex-$s$ fish in each age class ($N_{s,a}$, $a = 6, \ldots, n$, where $n$ refers to fish ages 30 and older) as a function of the number of age-6 female fish ($N_{f,6}$). Following Getz (1980), we assumed that

$$N_{s,a+1} = [\prod_{j=6}^{a} \exp(-Z_{s,j})]\, N_{f,6},$$

$$a = 6, \ldots, n-2 \tag{4}$$

$$N_{s,n} = [\prod_{j=6}^{n-1} \exp(-Z_{s,j})/(1 - \exp(-Z_{s,n})]\, N_{f,6} \tag{5}$$

where $Z_{s,j}$ was the total mortality rate for sex-$s$, age-$j$ fish. Using Equations (4) and (5), female spawning stock can be redefined as a function of $N_{f,6}$:

$$S_f = \sum_{a=6}^{n} N_{f,a}\, w_{f,a}\, p_{f,a} \tag{6}$$

$$= N_{f,6}[w_{f,6}\, p_{f,6} + \sum_{a=7}^{n-1} w_{f,a}\, p_{f,a} \prod_{j=6}^{a-1} \exp(-Z_{f,j})$$

$$+ w_{f,n}\, p_{f,n} \prod_{j=6}^{n-1} \exp(-Z_{f,j})/(1 - \exp(-Z_{f,n})] \tag{7}$$

$$= N_{f,6}\, \phi(F) \tag{8}$$

where $\phi(F)$ is the bracketed expression in Equation (7) for a specified $F$. We then substituted ($N_{f,6}\, \phi(F)$) for $S_f$ and solved Equation (3) for the equilibrium recruitment level as a function of $F$:

$$N_{f,6} = (0.5\, N_6[0]\, \phi(F) - S_f[0]$$

$$+ AS_f[0]/(A\, \phi(F)). \tag{9}$$

The virgin spawning stock $S_f[0]$ was calculated from Equations (4) to (6) for the specified level of $M$ and virgin recruitment. We used Equations (4)–(9) to calculate the equilibrium number-at-age vector and associated yield for $F$s from 0.0 to 0.5.

Following Francis (1986), we defined the target fishing mortality rate as $F_{0.1}$ for the constant recruitment case and $F_{\text{msy}}$ for the density-dependent case. $F_{0.1}$ was the fishing mortality rate at which the slope of the yield curve was one-tenth the slope of the curve at the origin (Gulland and Boerma 1973). Compared to managing for maximum sustained yield, the $F_{0.1}$ policy usually results in greater economic efficiency when constant recruitment is assumed (Gulland and Boerma 1973; Sissenwine 1981; Francis 1986). An additional advantage is that a larger spawning stock would be maintained (Sissenwine 1978). The less conservative $F_{\text{msy}}$ policy was assumed to be appropriate for the more conservative density-dependent case. The recommended yields for the constant recruitment and density-dependent cases were the equilibrium yields at $F_{0.1}$ and $F_{\text{msy}}$ respectively.

## RESULTS AND DISCUSSION

Our approach for estimating virgin recruitment level was similar to stock reduction analysis (SRA) (Kimura et al. 1984; Kimura 1985) except that we used a more general model to represent stock dynamics. In both approaches, a model is fully specified and the sequence of $F$s used to drive the model are those that would have produced the observed sequence of catches. A range of solutions can be obtained corresponding to a range of virgin recruitment levels, but the solution set can be restricted by comparing model predictions to auxiliary data.

We obtained similar 9-yr patterns of $F$ at different levels of virgin recruitment, particularly at higher recruitment levels where $F$s were low in all years (Fig. 1). For that reason, correlation coefficients were similar over a wide range of recruitment levels (Fig. 2). Stronger conclusions about the true level of virgin recruitment may be possible once additional years of catch and CPUE data become available.

Based on commercial snapper reel CPUE data, the virgin recruitment level that maximized the correlation between estimates of $F$ and fishing effort ranged from 30,000 to 100,000, depending on the assumed selectivity parameters and level of natural mortality (Table 4, Fig. 2). Correlations were high at all virgin recruitment levels, with maximum values obtained at the lowest recruitment levels capable of sustaining the 1978–86 observed catches (in order to match the sharp decline in CPUE from 1980 to 1982). Estimates based on research cruise CPUE data were higher, ranging from 40,000 to 180,000 (Table 5, Fig. 2). In both cases, the results were much more sensitive to $M$ than to the $L50_{Sel}$ parameter of the selectivity function (Tables 4, 5).

Based on these estimates of the virgin recruitment level, the adult population prior to fishing would have ranged from 287,000 to 452,000 fish (commercial CPUE) or 420,000 to 814,000 fish (research CPUE). Assuming 476 km$^2$ of tilefish habitat off South Carolina and Georgia (Low et al. 1983), the estimated density prior to fishing would have been 603–950 (commercial CPUE) or 883–1,710 (research CPUE) per km$^2$. We are not aware of other estimates of tilefish density prior to fishing. Submersible dives were made on the South Carolina tilefish grounds after the period of (assumed) heavy exploitation; unfortunately, no density estimates are currently available. Comparisons with the exploited MAB stock are of some interest because MAB catch rates in the late 1970s were similar to initial catch rates off South Carolina and Georgia (Low et al. 1983). Our density estimates were similar to the burrow density estimates from the MAB. Grimes et al. (1986) reported that burrow density in Hudson Canyon ranged from 1,815 per km$^2$ in 1980 to 1,132 in 1982. Estimates for Veatch Canyon ranged from 772 per km$^2$ in 1981 to 1,531 in 1984. Tilefish density in the MAB may be lower than these estimates because not all burrows may be occupied (Able et al. 1982). In addition, burrow density is highly variable (Able et al. 1987) and some burrows may be inhabited only during certain seasons, depending on water temperature (Grimes et al. 1986). Nevertheless, these comparisons suggest that the density estimates we generated from catch data were reasonable.

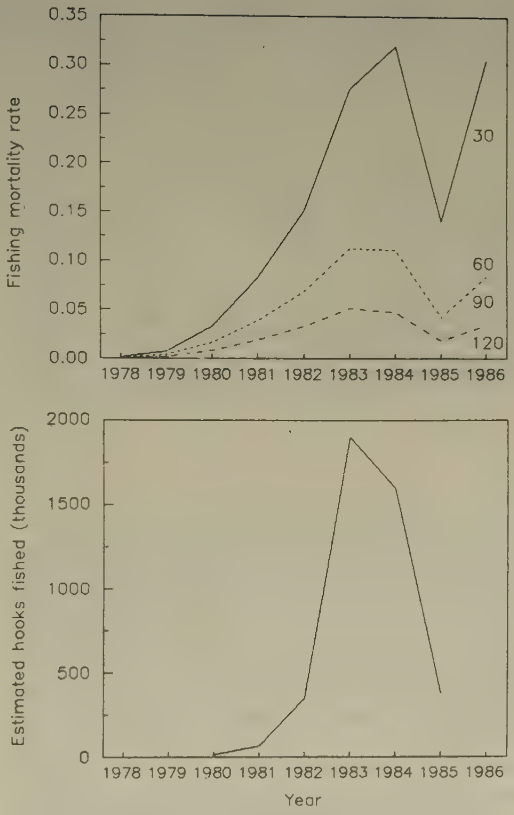

FIGURE 1.—Upper panel: estimated fishing mortality rates ($F$) from 1978 to 1986 at four (arbitrarily selected) levels of virgin recruitment (30,000–120,000 age-6 tilefish), assuming a natural mortality rate ($M$) of 0.10. Year-to-year changes in $F$ were similar at other levels of $M$. Lower panel: estimates of fishing effort (hooks fished) based on commercial (1980–81) and research (1982–85) CPUE data.

TABLE 4.—Estimates of virgin levels of recruitment, adult population density, and biomass; recommended levels of fishing mortality, biomass, and yield; and 1987 biomass. Estimates were obtained from commercial CPUE data, using two sets of selectivity ($L50_{Sel}$) parameters, four levels of natural mortality (*M*), and two assumptions about the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant).

| | Female/male selectivity parameter $L50_{Sel}$ | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 475/500 mm SL | | | | 500/525 mm SL | | | |
| *M*: | 0.10 | 0.15 | 0.20 | 0.25 | 0.10 | 0.15 | 0.20 | 0.25 |
| Virgin recruitment level (thousands) | 30 | 40 | 70 | 90 | 30 | 40 | 70 | 100 |
| Virgin population density (#/km$^2$) | 662 | 603 | 811 | 855 | 662 | 603 | 811 | 950 |
| Virgin biomass (t) | 1,574 | 1,128 | 1,266 | 1,160 | 1,574 | 1,128 | 1,266 | 1,288 |
| Recommended F (A = 0.889) | 0.10 | 0.15 | 0.23 | 0.33 | 0.13 | 0.20 | 0.30 | 0.48 |
| Recommended F (A = 1.000) | 0.10 | 0.16 | 0.23 | 0.32 | 0.11 | 0.17 | 0.25 | 0.34 |
| Recommended biomass (t) (A = 0.889) | 553 | 437 | 511 | 485 | 509 | 408 | 504 | 535 |
| Recommended biomass (t) (A = 1.000) | 678 | 524 | 636 | 628 | 700 | 551 | 680 | 753 |
| Recommended yield (t) (A = 0.889) | 41 | 40 | 57 | 62 | 42 | 42 | 58 | 70 |
| Recommended yield (t) (A = 1.000) | 51 | 51 | 72 | 78 | 52 | 51 | 70 | 82 |
| Estimated 1987 biomass (t) | 624 | 247 | 468 | 435 | 636 | 261 | 484 | 584 |

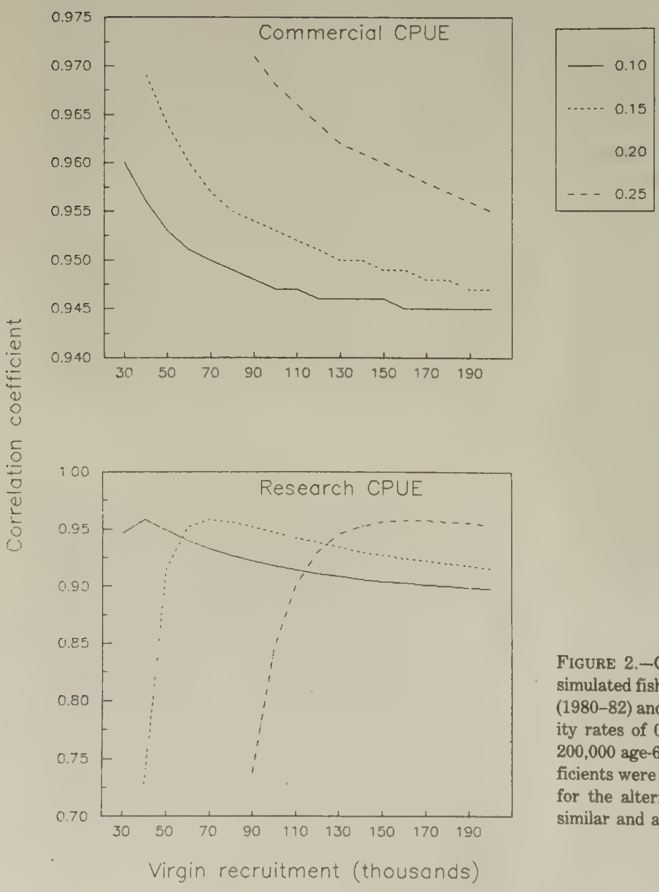

FIGURE 2.—Correlation between fishing mortality rates in the simulated fishery and estimates of fishing effort from commercial (1980–82) and research (1982–85) CPUE data, at natural mortality rates of 0.10–0.25 and virgin recruitment levels of 30,000–200,000 age-6 tilefish. Recruitment levels without correlation coefficients were inadequate to sustain the observed catches. Results for the alternative set of selectivity parameters ($L50_{Sel}$) were similar and are not shown here.

TABLE 5.—Estimates of virgin levels of recruitment, adult population density, and biomass; recommended levels of fishing mortality, biomass, and yield; and 1987 biomass. Estimates were obtained from research CPUE data, using two sets of selectivity ($L50_{Sel}$) parameters, four levels of natural mortality (*M*), and two assumptions about the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant).

| | Female/male selectivity parameter $L50_{Sel}$ | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 475/500 mm SL | | | | 500/525 mm SL | | | |
| *M*: | 0.10 | 0.15 | 0.20 | 0.25 | 0.10 | 0.15 | 0.20 | 0.25 |
| Virgin recruitment level (thousands) | 40 | 70 | 110 | 160 | 40 | 70 | 120 | 180 |
| Virgin population density (#/km$^2$) | 883 | 1,056 | 1,275 | 1,520 | 883 | 1,056 | 1,391 | 1,710 |
| Virgin biomass (t) | 2,098 | 1,974 | 1,989 | 2,062 | 2,098 | 1,974 | 2,170 | 2,319 |
| Recommended F (A = 0.889) | 0.10 | 0.15 | 0.23 | 0.33 | 0.13 | 0.20 | 0.30 | 0.47 |
| Recommended F (A = 1.000) | 0.10 | 0.16 | 0.23 | 0.32 | 0.11 | 0.17 | 0.25 | 0.34 |
| Recommended biomass (t) (A = 0.889) | 738 | 765 | 802 | 863 | 679 | 713 | 864 | 962 |
| Recommended biomass (t) (A = 1.000) | 904 | 917 | 999 | 1,117 | 932 | 965 | 1,165 | 1,355 |
| Recommended yield (t) (A = 0.889) | 55 | 71 | 89 | 109 | 56 | 73 | 100 | 126 |
| Recommended yield (t) (A = 1.000) | 69 | 90 | 114 | 139 | 70 | 89 | 120 | 148 |
| Estimated 1987 biomass (t) | 1,152 | 1,107 | 1,203 | 1,354 | 1,164 | 1,121 | 1,400 | 1,627 |

The two sets of CPUE estimates resulted in different conclusions about the current status of the stock. Based on commercial CPUE data, 1987 stock biomass was 22–45% of virgin biomass and 51–105% of the recommended level (Table 4). Estimated fishing mortality rates increased from about 0.1 in 1981 to a range of 0.3–1.4 in 1986 (Fig. 3). Based on research CPUE data, 1987 stock biomass was 55–70% of virgin biomass and 132–145% of the recommended level (Table 5). Estimated fishing mortality rates were much lower than from commercial CPUE data, increasing from about 0.08 in 1981 to 0.2 in 1986 (Fig. 3).

We believe that the results obtained from commercial CPUE data are far more likely, given recent reported declines in directed fishing. The decrease in landings observed in 1985 was attributed in part to reduced fishing pressure. A large group of boats from the Port Canaveral, FL area left the fishery, and a number of Georgia vessels began fishing further north (M. V. Rawson[3]). As of April 1988, most South Carolina longline vessels had switched to other fisheries and little directed tilefish fishing was occurring (R. Low[4]).

The difference in results for commercial and research CPUE estimates may be due to differences in areas fished. The RV *Georgia Bulldog* cruises were exploratory in nature, and catches were obtained primarily in the southern section of tilefish habitat off the Georgia coast (Harris and Grossman 1985). Early commercial effort was concentrated in the more northerly part of the tilefish habitat (Low et al. 1983). We recognize the commercial catch data provide a biased measure of abundance. Nevertheless, because South Carolina landings predominated in the developing fishery, we believe that commercial catch data from the primary fishing grounds will be a better overall measure of changes in abundance. For that reason, we restrict our remaining comments to results from the commercial CPUE data. Declines in commercial CPUE may underrepresent actual declines in abundance because fishermen presumably would change tactics over time in order to maintain high catch rates. If so, our use of commercial catch data may result in an optimistic estimate of current abundance.

We obtained equivalent estimates of 1987 biomass for the constant recruitment and density-dependent cases because of the short length of the data series, relative to the 6-yr lag between a reduction in spawning stock and subsequent lower recruitment to the fishery. Equilibrium yield curves differed substantially for the two recruitment assumptions (Fig. 4). Despite differences in equilibrium yield, recommended *F*s were very similar for the two cases because of the different criteria used to develop *F* and yield recommendations (Table 4). Recommended yield was moderately higher under the optimistic constant recruitment assumption (Table 4). Recommended *F* was higher when $L50_{Sel}$ was increased; however, differences in recommended yield were negligible.

Estimated *F*s differed substantially for the four levels of natural mortality (upper panel, Fig. 3). The large differences in 1984–86 *F*s probably were due

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[3] M. V. Rawson, University of Georgia Marine Extension Service, Brunswick, GA 31523, pers. commun. March 1987.

[4] R. Low, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. April 1988.

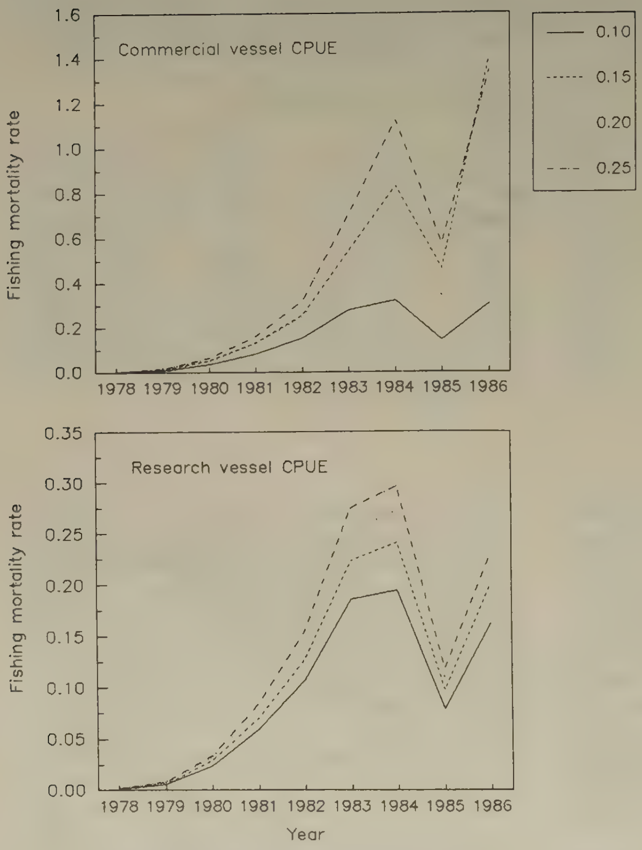

FIGURE 3.—Estimated fishing mortality rates ($F$) from 1978 to 1986 at natural mortality rates of 0.10–0.25. At each level of natural mortality, the virgin recruitment level was determined based on the correlation between $F$ and estimated fishing effort, where estimates of effort were based on commercial vessel or research vessel CPUE. Results for the alternative set of selectivity parameters ($L50_{Sel}$) were similar and are not shown here.

to the lack of CPUE estimates for those years. Virgin biomass levels were similar at different levels of $M$, ranging from 1,130 t at $M = 0.15$ to 1,570 t at $M = 0.10$ (Table 4). Estimates of 1987 biomass were somewhat similar and relatively low, ranging from 247 t at $M = 0.15$ to 636 t at $M = 0.10$ (Table 4). Equilibrium yield curves differed in a predictable way at different levels of $M$ (Fig. 4). Except at low $F$s (<0.10), equilibrium yield increased as $M$ increased, due to the higher estimates of virgin recruitment at higher levels of $M$. Recommended $F$ was higher at higher levels of $M$, ranging from 0.10 at $M = 0.10$ to 0.48 at $M = 0.25$ (Table 4). Recommended yield increased from 41–52 t at $M = 0.10$ to 62–82 t at $M = 0.25$.

These results demonstrate that an important source of uncertainty in assessing tilefish stock status is the estimate of $M$. Harris and Grossman (1985) obtained 1982–83 catch curve estimates of $Z$ equal to 0.25 for both female and male tilefish. Because the areas sampled by the RV *Georgia Bulldog* were thought to have received little fishing pressure, $M$ could be as high as 0.25. Catch curve estimates of $Z$ would be biased, however, if vulnerability to fishing increased with size. Turner et al. (1983) reported a decline in size at recruitment in the expanding MAB fishery and suggested that when larger tilefish were present, smaller ones either were less vulnerable to the gear or were avoided by fishermen. $Z$ (and $M$) could be underestimated if vulnerability to fishing increased with size. Alternatively, $Z$ (and $M$) could be overestimated if significant catches of predominantly older fish were made in the areas sampled by the RV *Georgia Bulldog*.

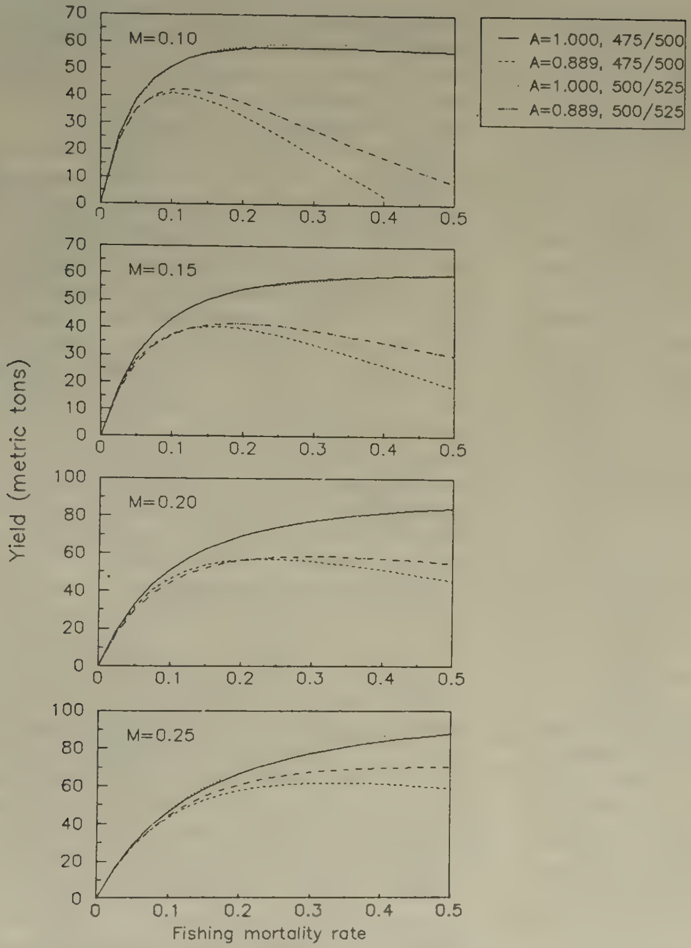

FIGURE 4.—Estimated equilibrium yield at four rates of natural mortality ($M$), two assumptions regarding the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant), and two values for the female and male (F/M) selectivity parameter $L50_{Sel}$.

Evidence that *M* is less than 0.25 was provided by predictive models used to estimate *M* from the growth rate ($k$) and maximum age (Alverson and Carney 1975) or from $k$, $L_\infty$, and mean water temperature (Pauly 1980). Estimates from the Alverson-Carney model were 0.107 (female) and 0.118 (male), whereas estimates from Pauly's method were 0.175 (females) and 0.163 (males) (Harris and Grossman 1985). Furthermore, Hoenig (1983) provided a model that predicts total mortality rate ($Z$) as a function of maximum age. Maximum observed age from May 1982 to August 1983 samples was 32 for female and 33 for male tilefish (Harris and Grossman 1985). Using Hoenig's model, $Z$ would be 0.13 for each sex; therefore, that would be a maximum estimate of *M*.

A potential source of error in this assessment is the assumption that the selectivity pattern is constant over time. Recent observations (R. Low, fn. 4) indicate that the size at first vulnerability to fishing has decreased from about 1 kg (Harris and Grossman 1985) to about 0.45 kg. The decreasing size at recruitment increases the likelihood of recruitment overfishing because fish are being harvested well before the size at maturity (about 2–3 kg for females). Thus, the current model probably underestimates the impact of fishing. Higher *F*s could be sustained if small tilefish were not vulnerable to fishing; unfortunately, it is difficult to regulate age at entry for hook-and-line gear (Myhre 1974) and discard mortality under a minimum size regulation would likely be substantial (Huntsman and Manooch 1978a).

A second potential source of error is the use of a deterministic model to represent recruitment. Changes in population size and CPUE are due not only to the impact of fishing but also to fluctuations in year-class strength. Because the estimates of virgin recruitment were based on changes in CPUE, fluctuations in recruitment that increase (decrease) the decline in CPUE would result in a lower (higher) estimate of virgin recruitment. Based on size-frequency data from the MAB tilefish fishery, Turner et al. (1983) suggested that fluctuations in tilefish year-class strength may be substantial. Using size- and age-frequency data collected off Georgia, Harris and Grossman (1985) found little evidence for strong fluctuations in year-class strength. Tilefish are somewhat difficult to age, however, so differences in year-class strength could be hidden by ageing errors.

A third source of error is the unknown number of fish caught off South Carolina or Georgia, but landed in Florida. The impact on the assessment would depend on the magnitude of the catches and the years in which the catches occurred. If we arbitrarily assume that actual annual removals were 25% higher than combined South Carolina-Georgia landings, recommended *F*s would be unchanged, whereas estimates of virgin recruitment and recommended yield would increase by about 25%. Thus, if Florida removals could be accounted for, estimates of stock size would be more accurate, but the increase in recommended yield would be offset by the increased catches, and would not result in increased overall landings.

## CONCLUSIONS

The results of this study provide estimates of the relationship between yield and fishing mortality and of the recommended level for *F*. Results obtained using commercial CPUE estimates indicate that sustainable harvests from the fishery are quite low, and would be obtained at *F*s considerably lower than observed in the developing fishery. We obtained higher estimates of population size and sustained yield using research CPUE data; however, we believe that the commercial CPUE data better reflect population trends. We estimate that current stock size is about 200–600 t, compared with a recommended level of 400–800 t. If the stock could be rebuilt to the recommended level, it should support an annual harvest of about 50 t. A rebuilding strategy is feasible for tilefish because catches are low except when directed fishing occurs (G. Ulrich[5]). At present, however, there are no restrictions on the tilefish fishery and despite reductions in effort, catches are probably large enough to prevent the stock from rebuilding (G. Ulrich fn. 5).

Apparent limitations on sustainable yield of the tilefish fishery probably can be attributed to the demographic characteristics of the stock. In a typical fishery for a long-lived, slow-growing species, a few years of high catches are followed by a sharp decline and a subsequent period of low yield (Huntsman and Manooch 1978b; Leaman and Beamish 1984; Francis 1986). Long-lived, sedentary species, such as reef fishes, may be particularly vulnerable to overfishing, even though fishing intensity may be low or the method inefficient (Huntsman and Manooch 1978b). Because tilefish are long-lived, slow-growing, and sedentary (due to their dependence on the availability of shelter), a similar pattern of exploitation can be expected for the tilefish fishery off South Carolina and Georgia.

Leaman and Beamish (1984) recommended that conservative harvest strategies be developed for long-lived species until the evolutionary implications of longevity are better understood. They suggested that extreme longevity (>50 years) may be an adaptive response to ensure population persistence under reproductive uncertainty. For example, a long reproductive life might enable a species to inhabit deeper water (200–1,000 m) where few competitors or predators are found, even though recruitment into such areas may be highly variable (Leaman and Beamish 1984). If variability in recruitment has a significant effect on tilefish stocks, a conservative management strategy emphasizing maintenance of a range of age classes may be appropriate.

## ACKNOWLEDGMENTS

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[5] G. Ulrich, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. July 1987.

their observations on the current status of the fishery.

## LITERATURE CITED

ABLE, K. W., C. B. GRIMES, R. A. COOPER, AND J. R. UZMANN.
1982. Burrow construction and behavior of tilefish, *Lopholatilus chamaeleonticeps*, in Hudson Submarine Canyon. Environ. Biol. Fishes 7:199–205.

ABLE, K. W., D. C. TWICHE, C. B. GRIMES, AND R. S. JONES.
1987. Sidescan sonar as a tool for detection of demersal fish habitats. Fish. Bull., U.S. 85:725–736.

ALVERSON, D. L., AND M. J. CARNEY.
1975. A graphic review of the growth and decay of population cohorts. J. Cons. int. Explor. Mer 36:133–143.

DERISO, R. B., T. J. QUINN II, AND P. R. NEAL.
1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

ERICKSON, D. L., AND G. D. GROSSMAN.
1986. Reproductive demography of tilefish from the South Atlantic Bight with a test for the presence of protogynous hermaphroditism. Trans. Am. Fish. Soc. 115:279–285.

FAHAY, M. P., AND P. BERRIEN.
1981. Preliminary description of larval tilefish (*Lopholatilus chamaeleonticeps*). Rapp. P.-v. Réun., Cons. int. Explor. Mer 178:600–602.

FRANCIS, R. C.
1986. Two fisheries biology problems in west coast groundfish management. North Am. J. Fish. Manage. 6:453–462.

FREEMAN, B. L., AND S. C. TURNER.
1977. Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps* (Goode and Bean). U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, Tech. Serv. Rep. No. 5, 41 p.

GETZ, W. M.
1980. Harvesting models and stock recruitment curves in fisheries management. *In* W. M. Getz (editor), Mathematical modelling in biology and ecology, p. 284–304. Springer-Verlag, Berlin, Germany.

GRIMES, C. B., K. W. ABLE, AND R. S. JONES.
1986. Tilefish, *Lopholatilus chamaeleonticeps*, habitat, behavior and community structure in Mid-Atlantic and southern New England waters. Environ. Biol. Fishes 15:273–292.

GRIMES, C. B., K. W. ABLE., AND S. C. TURNER.
1980. A preliminary analysis of the tilefish, *Lopholatilus chamaeleonticeps*, fishery in the Mid-Atlantic Bight. Mar. Fish. Rev. 42(11):13–18.

GROSSMAN, G. D., M. J. HARRIS, AND J. E. HIGHTOWER.
1985. The relationship between tilefish, *Lopholatilus chamaeleonticeps*, abundance and sediment composition off Georgia. Fish. Bull., U.S. 83:443–447.

GULLAND, J. A.
1971. Science and fishery management. J. Cons., Cons. int. Explor. Mer 33:471–477.

GULLAND, J. A., AND L. K. BOEREMA.
1973. Scientific advice on catch levels. Fish. Bull., U.S. 71:325–335.

HARRIS, M. J., AND G. D. GROSSMAN.
1985. Growth, mortality, and age composition of a lightly exploited tilefish (*Lopholatilus chamaeleonticeps*) substock off Georgia. Trans. Am. Fish. Soc. 114:827–836.

HENNEMUTH, R. C.
1979. Man as predator. *In* G. P. Patil and M. Rosenzweig (editors), Contemporary quantitative ecology and related econometrics, p. 507–532. Int. Stat. Ecol. Program, Stat. Ecol. Series, Vol. 12.

HENRY, F. D., JR.
1986. Status of the coastwide chilipepper (*Sebastes goodei*) fishery. *In* Status of the Pacific coast groundfish fishery and recommendations for management in 1987. Pacific Fishery Management Council, Portland, OR.

HIGHTOWER, J. E., AND W. H. LENARZ.
1986. Status of the widow rockfish fishery. *In* Status of the Pacific coast groundfish fishery and recommendations for management in 1987. Pacific Fishery Management Council, Portland, OR.

HOENIG, J. M.
1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull., U.S. 81:898–903.

HUNTSMAN, G. R., AND C. S. MANOOCH III.
1978a. Minimum size limits for reef fishes. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 32:509–513.
1978b. Coastal pelagic and reef fishes in the South Atlantic Bight. *In* Henry Clepper (editor), Marine recreational fisheries, No. 3, p. 97–106. Proceedings of the Second Annual Marine Recreational Fisheries Symposium; Sport Fishing Institute, Washington, D.C.

KATZ, S. J., C. B. GRIMES, AND K. W. ABLE.
1983. Delineation of tilefish, *Lopholatilus chamaeleonticeps*, stocks along the United States east coast and in the Gulf of Mexico. Fish. Bull., U.S. 81:41–50.

KIMURA, D. K.
1985. Changes to stock reduction analysis indicated by Schnute's general theory. Can. J. Fish. Aquat. Sci. 42: 2059–2060.
1988. Stock-recruitment curves as used in the stock-reduction analysis model. J. Cons. int. Explor. Mer 44:253–258.

KIMURA, D. K., J. W. BALSIGER, AND D. H. ITO.
1984. Generalized stock reduction analysis. Can. J. Fish. Aquat. Sci. 41:1325–1333.

LEAMAN, B. M., AND R. J. BEAMISH.
1984. Ecological and management implications of longevity in some northeast Pacific groundfishes. Int. North Pac. Fish. Comm., Bull. 42, p. 85–97.

LENARZ, W. H., AND J. E. HIGHTOWER.
1985. Status of the widow rockfish fishery. *In* Status of the Pacific coast groundfish fishery and recommendations for management in 1986. Pacific Fishery Management Council, Portland, OR.

LOW, R. A., AND G. F. ULRICH.
1982. Reef fishes and associated management issues in South Carolina. S.C. Wildl. Mar. Resour. Dep. Educ. Rep. No. 14, 49 p.
1983. Deep-water demersal finfish resources and fisheries off South Carolina. S.C. Mar. Resour. Cent. Tech. Rep. No. 57, 24 p.

LOW, R. A., JR., G. F. ULRICH, AND F. BLUM.
1983. Tilefish off South Carolina and Georgia. Mar. Fish. Rev. 45(4–6):16–26.

METHOT, R. D.
In press. Synthetic estimates of historical abundance and mortality for nothern anchovy. *In* E. F. Edwards and B. A. Megrey (editors), Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. 6.

MOHN, R. K.
1983. Effects of errors in catch and effort data on tuning cohort analysis, with a postscript on logistic production models. *In* W. G. Doubleday and D. Rivard (editors), Sampling commercial catches of marine fish and invertebrates, p. 141–150. Can. Spec. Publ. Fish. Aquat. Sci. 66.

MYHRE, R. J.
1974. Minimum size and optimum age at entry for Pacific halibut. Int. Pac. Halibut Comm., Sci. Rep. 55, 15 p.

PAULY, D.
1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. int. Explor. Mer 39:175-192.

RIVARD, D.
1983. Effects of systematic, analytical, and sampling errors on catch estimates: a sensitivity analysis. *In* W. G. Doubleday and D. Rivard (editors), Sampling commercial catches of marine fish and invertebrates, p. 114-129. Can. Spec. Publ. Fish. Aquat. Sci. 66.

SISSENWINE, M. P.
1978. Is MSY an adequate foundation for optimum yield? Fisheries 3:22-24, 37-42.
1981. An overview of some methods of fish stock assessment. Fisheries 6:31-35.

TURNER, S. C., C. B. GRIMES, AND K. W. ABLE.
1983. Growth, mortality, and age/size structure of the fisheries for tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic-Southern New England region. Fish. Bull., U.S. 81:751-763.

VALENTINE, P. C., J. R. UZMANN, AND R. A. COOPER.
1980. Geology and biology of Oceanographer Submarine Canyon. Mar. Geol. 38:283-312.

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# TROPHIC RELATIONS OF THE BLUE ROCKFISH, *SEBASTES MYSTINUS*, IN A COASTAL UPWELLING SYSTEM OFF NORTHERN CALIFORNIA

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## ABSTRACT

The planktivorous *Sebastes mystinus* in nearshore habitats off northern California feeds primarily on relatively large, gelatinous zooplankters that originate offshore, including thaliaceans, ctenophores, and pelagic hydrozoans. These prey organisms increase in number during spring and summer when surface waters driven seaward by northerly winds carry upwelled nutrients to diatoms that nourish offshore zooplankton populations. But the resulting increases in zooplankton during this upwelling season become available to *S. mystinus* in the nearshore habitats only when the surface flow turns shoreward during intermittent episodes of downwelling. Although some of this shoreward flow is driven by southerly winds, much of it occurs during calms, or under northerlies lacking the velocities needed to drive surface waters seaward. There is increasing shoreward transport during fall and winter, when downwelling episodes are more frequent, but progressively fewer zooplankters are carried into the nearshore habitats. This is because as less nutrients come into the system with the reduced upwelling, and as available sunlight declines, the offshore zooplankton populations suffer from shortages of diatoms. Although *S. mystinus* compensates for decreased numbers of zooplankters during most of the year with increased consumption of specific plant materials, i.e., *Nereocystis sori*, or the monostromatic epiphytes *Porphyra nereocystis* and *Smithora naidum* (depending on the season), these too are in short supply during winter. In winter, therefore, *S. mystinus* experiences its poorest feeding conditions. Thus, *S. mystinus* is adapted to feeding opportunities created by alternating episodes of strong upwelling and strong downwelling, and is most abundant within its range along the west coast of North America where both conditions are well developed.

Coastal marine fishes in temperate latitudes experience major seasonal changes in their environment. In study off northern California's Mendocino coast (lat. 39°13′N, long, 123°14′W), we studied the effects of seasonal change on the trophic relations of the blue rockfish, *Sebastes mystinus* (Fig. 1). *Sebastes mystinus*, a major species in the recreational fishery off northern and central California (Frey 1971), is a planktivore that feeds on scyphozoans, ctenophores, copepods, amphipods, thaliaceans, fishes, and algae (Gotshall et al. 1965; Love and Ebeling 1978; Hallacher and Roberts 1985). Although its diet is known to vary with the season, relationships involving specific environmental features, and the availability of prey, remain unclear.

The marine environment off California is profoundly affected by seasonal variations in wind-driven movement of the surface water (Reid et al. 1958; Bolin and Abbott 1962; Bakun and Parrish 1980). This force, known as Ekman transport (Ekman 1905), is strongest off the Mendocino coast (Bakun 1973), where it must be a major influence on the trophic relations of *S. mystinus*. Because Ekman transport is the basis of coastal upwelling (e.g., Smith 1968), it is of great importance to biological productivity (e.g., Boje and Tomczak 1978) and, therefore, to the availability of food.

Upwelling develops along the coast of northern California when surface waters driven seaward by northerly winds, such as those characteristic of spring and summer, are replaced by colder subsurface waters from offshore that flow up into the nearshore habitat (Smith 1968; Bakun 1973). On the other hand, an opposing condition develops when surface waters driven shoreward by southerly winds, such as those characteristic of winter storms, flow over the colder nearshore waters to produce the condition sometimes called downwelling (Bakun 1973). But despite the strong seasonality evident in both upwelling and downwelling, short-term reversals lasting just a few days occur throughout the year (see Bakun [1973] and Mason and Bakun [1986]).

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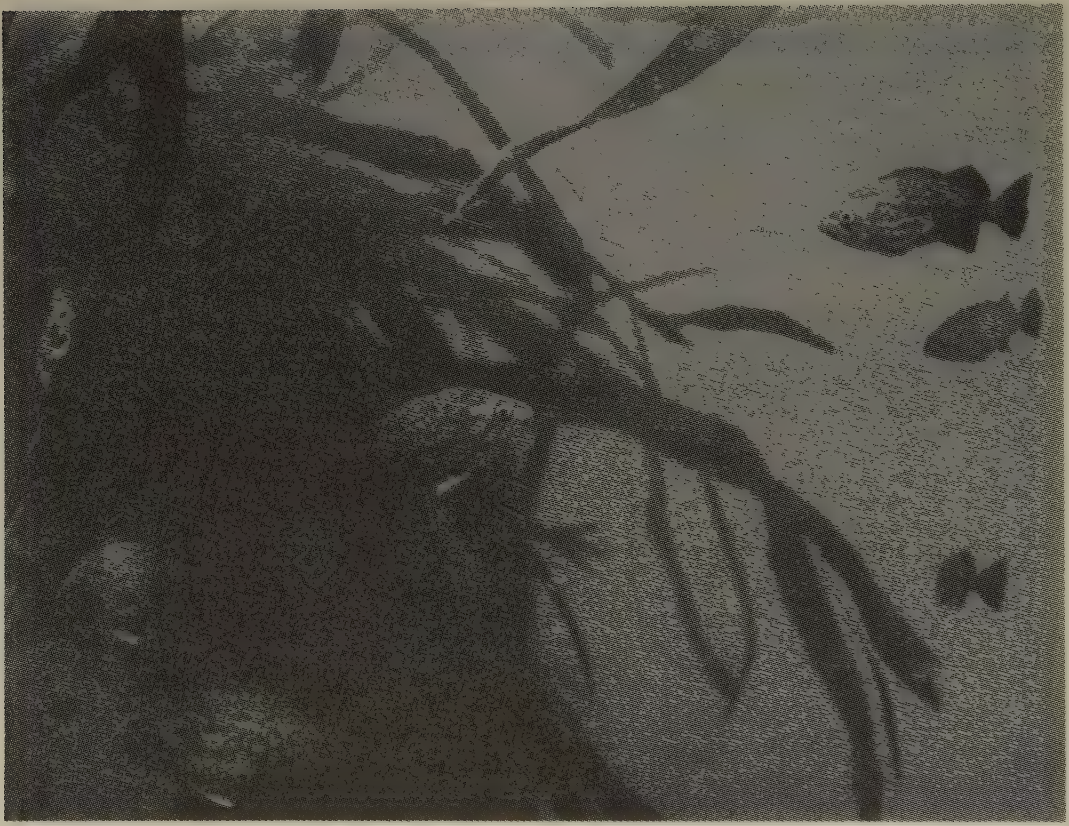

FIGURE 1.—*Sebastes mystinus* next to canopy of bull kelp, *Nereocystis leutkeana*, off Mendocino.

In this paper we consider how the trophic relations of *S. mystinus* respond as seaward and shoreward movements of the surface water produce alternating episodes of upwelling and downwelling. Emphasis is on how the resulting environmental changes alter the relative availability of food. Among studies of marine fishes, this is, to our knowledge, the most comprehensive attempt yet made to integrate data on food, potential food, and environmental variables—all key elements in trophic relations.

## METHODS

The study lasted from the winter of 1976–77 to the summer of 1981, with the first 15 months involving exploratory work along about 15 km of the Mendocino coast south of Point Cabrillo. A study site was then established off Salmon Point (Fig. 2) during the spring of 1978, and from that time sampling followed a set regime.

### Study Site

The study site (Fig. 3) was in 10–15 m of water, about 300 m from shore. Rocks the size of houses jutted 10–15 m above the water at the seaward perimeter of the site, but despite the shelter offered by these rocks, most of the area was regularly swept by wind and sea. Except for isolated pockets of sand, the site was floored by rock pavement and boulders (some 5–15 m in diameter), largely swept clean by the turbulence and surge that prevailed most of the time.

### Environmental Variables

During each sampling session, we noted the gen-

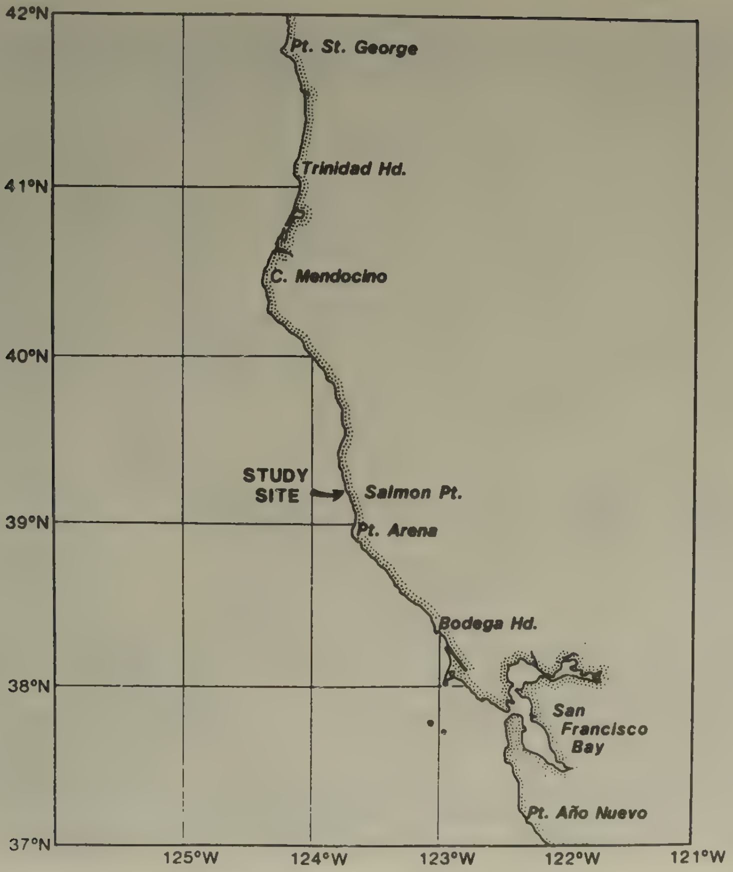

FIGURE 2.—The coast of northern California.

eral state of the weather, including wind direction and estimated velocity. In this paper (except in Figures 4 and 9, as noted below) we consider winds from between northwest and northeast to be "northerly", and from between SW and SE to be "southerly". We also noted sea conditions and recorded sea-surface temperatures. More precise wind data became available after May 1980, when a NOAA weather station was established at Mendocino. During the same month, we placed recording thermographs at depths of 6 and 20 m in the study area, and although the deeper site was abandoned after 1981 in favor of replicating the record with two instruments at the shallower site, these have given us a continuous record of water temperatures from then until the present (Spring of 1988). Based on these observations and in situ visual assessments of the plankton and water characteristics, usually we could tell whether upwelling or downwelling predominated during a sampling session even though most of the time conditions were to some extent mixed.

## Diet and Occurrences of Food

To relate the diet of *S. mystinus* to foods present at the time of feeding, we took concurrent samples of gut contents and plankton, as well as some selective samples of the benthos. Complications from normal diel variability were reduced by taking all samples between the hours of 1100 and 1300. The sampling schedule was strongly influenced by the weather, as much of the time work was prevented by high seas and/or long-period swells and result-

FIGURE 3.—Study site off Salmon Point.

ing turbulence. Although all seasons were sampled, most collections and observations were made when the sea was relatively calm, a condition that generally lasted no more than a few days at a time. Nevertheless, because often the weather turned while observations were under way, turbulent conditions were well represented.

### Fish

The *S. mystinus* studied at Mendocino were spatially segregated by size and age. This paper considers only adult fish of more than 200 mm SL, which forage by day in aggregations of up to several hundred individuals in the upper levels of the water column. The analysis of gut-contents involved 247 individuals, 200–350 mm SL, taken from these aggregations using handheld spears. Juveniles and subadults are excluded because they forage at lower levels of the water column and consume organisms not taken by adults.

### Plankton

Most sampling sessions included two plankton collections: one at the sea surface, and the other between 1 and 2 m above the sea floor. Only the 27 surface collections are considered here, however, because the others sampled at levels of the water column below where adults usually feed. For each collection we used scuba to push the net (0.333 mm mesh in a 78 cm × 78 cm frame) through the water for 5 minutes. Occasionally the net broke the surface, but usually was kept underwater to avoid fouling the sample with floating debris. (See Hobson and Chess 1976 for additional information on this procedure, and how the samples were processed and analyzed.) We visually assessed the larger zooplankters in the water column during each collection, as well as at other times during each sampling session, and these observations greatly enhanced our ability to interpret the samples.

### Benthos

Although *S. mystinus* is a planktivore, it is important to include the benthos when documenting environmental changes that affect its feeding. Many of the actual or potential foods of *S. mystinus* originate on the underlying substrata, and their occurrences in the water column relate to changes in the benthos. Thus, assessments of the benthos done during other studies concurrently under way in the study area, including visual counts and airlift samples, produced data that are incorporated into this report where pertinent.

### Ranking Prey Taxa

To estimate the relative importance of the various prey organisms in the diet of *S. mystinus*, we grouped related forms in multispecies categories that were then ranked. The ranking was based on an index calculated as: relative frequency of occurrence in diet × mean number of individuals consumed × percent of total diet volume that was represented by that category. This index is similar to the widely used Index of Relative Importance (IRI) of Pinkas et al. (1971), but puts more weight on numbers consumed. It is important to emphasize numbers consumed in quantifying the feeding activity of *S. mystinus* (and most other planktivores) because the many small prey are ingested individually, making the capture of each a discrete act.

## RESULTS

During the four years of this study, spring and (to a lesser extent) summer constituted an upwelling season, while fall and (to a greater extent) winter constituted a downwelling season. The spring transition between downwelling and upwelling seasons occurred over just a few days between late March and early April, whereas the less distinct fall transition between upwelling and downwelling seasons was extended over a month or more between mid-August and late October.

Despite this seasonal pattern, however, there were short-term reversals of just a few days that had profound effects. Reactions of the environment to major wind changes were virtually immediate. Sharply reduced water temperatures signifying the intrusion of upwelled water often followed within hours of increased northerly winds, while warmer water rich in such readily visible zooplankters as ctenophores, hydrozoans, pteropods, thaliaceans, and larvaceans, often flowed into the nearshore habitats within a day after the onset of southerly winds. Conditions during each sampling session are listed in Table 1.

Although downwelling conditions were most intense under southerly winds, they also developed during calms and with weak northerlies. We found that generally it took northerlies of 10 knots (K) or more to produce upwelling conditions, although as little as 5 K were effective if held steady for several days. In the absence of sufficient force, however, upwelling ceased and warmer water rich in offshore zooplankters entered the nearshore habitat, generally moving in a southerly direction along the coast.

The close relation between shifts in prevailing wind and alternations between upwelling and downwelling is illustrated by comparing the wind direction and velocity measured by the nearby NOAA weather station to the sea temperatures recorded by our thermographs. Although these data became available only during the last year of the study, subsequent years have produced similar profiles (except 1982–83, when there was a strong El Niño). Thus, the pattern of sea temperatures and wind during the upwelling season of 1981 and during the downwelling season of 1980–81, recounted in detail below, are representative.

## The Upwelling Season

The upwelling season began in late March or early April with a precipitous drop in sea temperatures. It was a drop of about 3°C—typically from 11°–12°C to 8°–9°C—that coincided with the onset of strong, persistent northerly winds characteristic of this time of year. The pattern of sea temperatures and wind during the 1981 upwelling season (Fig. 4) illustrates how upwelling and downwelling related to prevailing winds during that period.

### Habitat Conditions

At the start of the upwelling season, the nearshore habitats appeared barren. Storm seas during the previous winter had carried away most of the bull

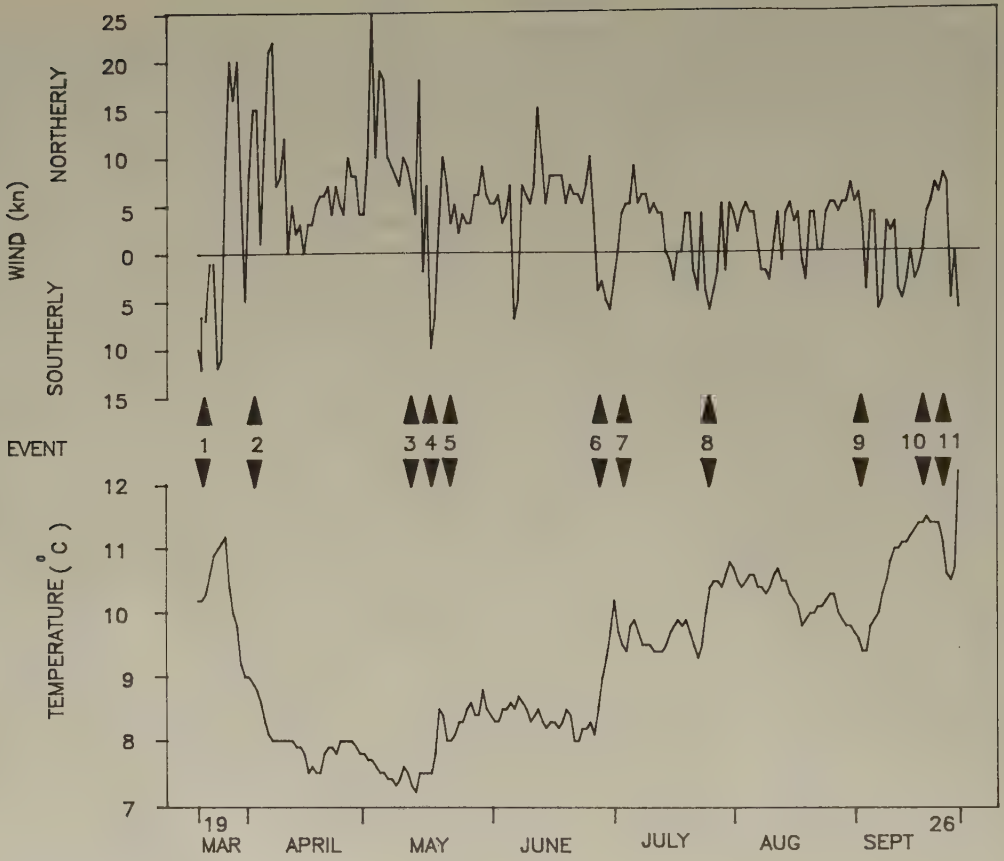

FIGURE 4.—Sea temperatures and wind off Mendocino during the 1981 upwelling season. *Plotted sea temperatures* are estimated daily means from record of continuously recording thermograph. Plotted wind velocities and directions are averages of 2–5 daily readings. Southerly values represent winds from south of east-west axis, northerly values represent winds from north of this axis. The highly infrequent winds from due west or due east were entered as zero. In calculating values for days of both northerlies and southerlies, the former were considered positive, the latter negative. The following accounts of events identified in the figure cite wind velocities that exceed plotted values, which are averages

EVENT 1—Seven days of southerly winds, 19–25 March, with sea temperatures rising to 11.1°C, represented the last downwelling episode of the 1980–81 downwelling season.

EVENT 2—The 1981 upwelling season began on 26 March, as 2 weeks of strong northerlies (to 4 April) resulted in an abrupt drop of more than 3°C in sea temperature.

EVENT 3—Water temperatures fell to the lowest point of the year, 7.3°C, on 13 May following over 2 weeks of 10–30 K northerlies.

EVENT 4—The first of a series of downwelling episodes during this upwelling season developed as 8–12 K southerlies on 17 and 18 May resulted in a sharp rise in sea temperature to 8.5°C.

EVENT 5—Temperatures dipped when the wind shifted back to the north on 19 May. Over the next month variable northerlies blew at less than 10 K, and although sea temperatures did not vary more than a few tenths of a degree, they were consistently about 1°C warmer than before the 17–18 May downwelling episode.

EVENT 6—On 28 June, the first of 6 consecutive days of 4–10 K southerlies, sea temperatures began a steep climb to above 10°C that marked the upwelling season's second major downwelling episode.

EVENT 7—Northerlies returned on 3 July, and sea temperatures immediately dropped below 10°C again. Despite northerlies of 5–7 K over the next 2 weeks, sea temperatures remained at about 9.5°C, again about 1°C warmer than before the 28 June–2 July downwelling episode.

EVENT 8—With southerlies of 5–10 K on 7 of the 9 days between 12 and 20 July, sea temperatures once again rose above 10°C to mark the season's third major downwelling episode.

TABLE 1.—Conditions during sampling sessions off Salmon Point, Mendocino County, 1978–81.

| | | | | Fish sampled | | |
|---|---|---|---|---|---|---|
| Date | Sea temp. (°C) | Wind dir. : vel. (knots) | Plankton condition[1] | No. | Size range (mm) | Mean (mm) |
| I. Upwelling season, upwelling conditions | | | | | | |
| 5/10/78 | 8.5 | NW: 10 | U/M | 7 | 270–312 | 289.7 |
| 8/08/78 | 10.5 | NW: 10 | U | 6 | 285–309 | 293.0 |
| 6/12/79 | 9.0 | NW: 15 | U/M | 7 | 241–312 | 239.3 |
| 6/24/80 | 10.0 | None | U | 9 | 224–308 | 250.0 |
| 4/09/81 | 8.1 | NW: 15 | U | 8 | 235–300 | 265.6 |
| 5/19/81 | 9.5 | WNW: 10 | U/M | 1 | 260 | 260.0 |
| 6/17/81 | 9.0 | NNW: 10 | U | 13 | 260–336 | 301.0 |
| II. Upwelling season, downwelling conditions | | | | | | |
| 6/21/78 | 9.0 | None | D/M | 3 | 228–308 | 270.3 |
| 6/29/78 | 10.0 | SW: 2 | D/M | 6 | 240–315 | 254.7 |
| 8/23/78 | 11.0 | None | D | 6 | 230–280 | 259.0 |
| 9/08/78 | 14.0 | None | D | 4 | 240–295 | 277.5 |
| 4/24/79 | 10.0 | None | M | 9 | 225–313 | 277.7 |
| 7/24/79 | 11.5 | None | M | 11 | 208–302 | 239.5 |
| 8/27/79 | 12.8 | NW: 5 | M | 12 | 204–335 | 264.6 |
| 5/29/80 | 9.5 | None | D/M | 20 | 213–330 | 276.4 |
| 7/17/80 | 11.0 | NW: 5 | D/M | 5 | 240–304 | 270.8 |
| 8/21/80 | 11.0 | S: 5 | D | 9 | 230–305 | 270.6 |
| III. Downwelling season, downwelling conditions, fall | | | | | | |
| 10/04/78 | 11.0 | WNW: 10 | D+ | 3 | 270–310 | 286.7 |
| 10/18/78 | 12.0 | S: 5 | D+ | 9 | 220–350 | 296.2 |
| 12/08/78 | 9.0 | S: 8 | D+ | 17 | 227–331 | 281.2 |
| 10/16/79 | 14.0 | NW: 8 | D | 13 | 218–311 | 280.1 |
| 11/04/80 | 12.0 | N: 6 | D | 17 | 230–335 | 296.6 |
| 12/17/80 | 12.0 | NNW: 5 | D | 14 | 225–331 | 276.3 |
| IV. Downwelling season, downwelling conditions, winter | | | | | | |
| 2/04/79 | 10 | S: 12 | D | 12 | 231–320 | 273.3 |
| 3/06/79 | 11 | W: 8 | D | 2 | 224–260 | 242.0 |
| 1/31/80 | 11 | None | M | 16 | 200–345 | 275.3 |
| 1/13/81 | 13 | SW: 5 | D | 8 | 275–305 | 286.3 |

[1] Plankton condition. D = Downwelling condition: zooplankters considered to be offshore species, especially relatively large gelatinous forms, numerous. U = Upwelling condition: offshore zooplankters absent. M = Mixed condition: some offshore zooplankters present.

kelp, *Nereocystis leutkeana*, which is the major component of the kelp forests. These same seas, often heavily laden with sediment, had also scoured the seafloor of much of the algal understory, as well as many of the sedentary invertebrates. Once the upwelling season had been established, however, the habitats changed rapidly.

Often during early-season upwelling the water was relatively transparent, although after rains visibility often was limited by suspended sediment discharged into the nearshore habitat from coastal streams. By mid-May, however, the numbers of planktonic diatoms (primarily *Chaetoceros* sp. and *Nitzchia* sp.) had greatly increased to depths of

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EVENT 9—In the last major upwelling of this upwelling season, sea temperatures fell to 9.4°C on 2 September after 10 consecutive days of 5–8 K northerlies.

EVENT 10—Sea temperatures rose steadily to 11.4°C on 17 September after 1–3 day periods of 4–8 K northerlies had alternated with 1–4 day periods of 4–8 K southerlies through the first half of that month.

EVENT 11—Sea temperatures fell to 10.5°C on 24 September after 7 consecutive days of 5–15 K northerlies. A shift to southerlies on 25 September started another climb, and the transition to the downwelling season clearly was under way. This transition, however, was not nearly so well defined as that which had introduced the upwelling season 6 months before.

10–20 m, which often limited visibility to a few meters. These diatom blooms were most evident during the intermittent episodes of downwelling. The benthos similarly proliferated. Within a few weeks after the initial upwelling, a growth of benthic diatoms (primarily *Isthmia nervosa* and *Tricertium americana*) appeared on the previously baron rocks, and even on sand sheltered from wave surge. Then larger elements of the biota began to increase in size and number. Particularly evident were calcareous sponges (especially *Leucosolenia* spp.), hydroids, and certain bryozoans. Benthic algae, predominantly *Desmarestia ligulata*, rapidly overgrew much of the rock substrata, while young *Nereocystis leutkeana*, which first appeared on the seafloor in May, had grown to the water's surface by mid-June. Swarms of mysids were increasingly numerous near the seafloor in April (they had been prominent for a month or more), and caprellid and gammaridean amphipods on rocky substrata began a sharp increase in numbers.

The bull kelp had formed a dense canopy by mid-July, and at about the same time large numbers of sori (reproductive structures) began falling from the kelp's fronds. (A frond that had recently lost a sorus appears at the left side of Figure 1.) Planktonic diatoms continued to proliferate during periodic blooms, but by this time the benthic diatoms that had carpeted much of the seafloor during the spring were mostly gone. Similarly, the mysid swarms, which had peaked in May and June, usually began to decline by mid-July. Other elements of the biota,

TABLE 2.—Food of adult *Sebastes mystinus* relative to near-surface plankton during upwelling episodes of the upwelling season: $n = 7$.

| Rank | Food organism | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 1 | PLANTS (3751.20) | **NR[2]** | **72** | **NR** | **52.1** | **NR** | **NR** | **NR** | **NR** |
| | *Nereocystis* sori | 15–20 | 15 | 1.10 | 10.6 | NR | NR | NR | NR |
| | *Porphyra* sp. | NR | 15 | NR | 9.9 | NR | NR | NR | NR |
| | *Smithora naidum* | NR | 21 | NR | 17.0 | NR | NR | NR | NR |
| | Others | NR | 21 | NR | 14.6 | NR | NR | NR | NR |
| 2 | PELAGIC HYDROZOA (1373.30) | **10–30** | **21** | **4.51** | **14.5** | **<1–4** | **86** | **120.08** | **2.3** |
| | Hydromedusae | | | | | | | | |
| | *Eutonina indicans* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others | — | 0 | 0.00 | 0.0 | <1–2 | 86 | 68.65 | 0.6 |
| | Syphonophora | | | | | | | | |
| | *Muggiaea atlantica* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | *Stephanomia bijuga* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others | — | 0 | 0.00 | 0.0 | 3–4 | 14 | 51.43 | 1.7 |
| | Chondrophora | | | | | | | | |
| | *Velella velella* | 10–30 | 21 | 4.51 | 14.5 | NA[3] | NA | NA | NA |
| 3 | MYSIDACEA (203.15) | **5–7** | **3** | **10.26** | **6.6** | **—** | **0** | **0.00** | **0.0** |
| | *Acanthomysis* spp.[4] | 5–7 | 3 | 10.26 | 6.6 | — | 0 | 0.00 | 0.0 |
| | Others | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| 4 | SCYPHOZOA (61.60)[5] | **NR** | **8** | **NR** | **7.7** | **NR** | **NR** | **NR** | **NR** |
| | Fragments | NR | 8 | NR | 7.7 | NR | NR | NR | NR |
| 5 | EUPHAUSIACEA (35.10) | **5–8** | **15** | **1.95** | **1.2** | **<1–4** | **57** | **363.60** | **3.1** |
| | Larvae | — | 0 | 0.00 | 0.0 | <1–4 | 57 | 363.60 | 3.1 |
| | *Thysanoessa* spp. | 5–8 | 15 | 1.95 | 1.2 | — | 0 | 0.00 | 0.0 |
| | Others | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| 6 | GAMMARIDEA (1.80) | **1–8** | **8** | **0.75** | **0.3** | **1–8** | **86** | **10.31** | **5.3** |
| | *Atylus tridens* | — | 0 | 0.00 | 0.0 | 2–8 | 29 | 4.63 | 5.0 |
| | *Ishyrocerus* n. sp. | 4 | 3 | 0.31 | 0.1 | — | 0 | 0.00 | 0.0 |
| | *Jassa falcata*[6] | 1–3 | 8 | 0.28 | 0.1 | <1–3 | 14 | 0.78 | NR |
| | *Polycheria osbourni* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others | 2–8 | 5 | 0.16 | 0.1 | 1–2 | 57 | 4.90 | 0.3 |
| 7 | CALANOIDA (0.90) | **5–6** | **8** | **0.16** | **0.7** | **<1–7** | **100** | **2454.09** | **38.6** |
| | Nauplii | — | 0 | 0.00 | 0.0 | <1 | 14 | 72.00 | 0.1 |
| | *Acartia* spp. | — | 0 | 0.00 | 0.0 | 1–2 | 52 | 224.23 | 4.4 |
| | *Calanus pacificus* | — | 0 | 0.00 | 0.0 | 2–3 | 57 | 24.68 | 5.3 |
| | *Eucalanus californicus* | 6 | 8 | 0.13 | 0.6 | 4–7 | 71 | 35.48 | 1.4 |
| | *Rhincalanus nasutus* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others[7] | 5 | 3 | 0.03 | 0.1 | <1–3 | 1 | 2097.70 | 27.4 |

however, reached maximum development during the summer. Prominent among them were benthic algae, e.g., *Desmarestia ligulata* and *Laminaria setchelli*, as well as certain sedentary animals including various sponges, e.g., *Leucilla nuttingi*; ascidians, e.g., *Trididemnum opacum*; hydroids, e.g., *Obelia* spp.; and bryozoans, e.g., *Bugula* spp. The benthic caprellids and gammarideans attained peak numbers during early summer, when they literally carpeted some areas of the seafloor. Samples taken with an airlift during July 1978 measured densities of over 10,000 caprellids (mostly *Metacaprella kennerleyi*), and 108,000 gammarids (mostly *Jassa* spp.) in m$^2$ quadrats. Their numbers declined sharply during August, however, and by September they occurred only in scattered patches.

### Feeding Conditions

The diet of *S. mystinus* relative to foods present during the upwelling season was assessed with samples of gut contents and near-surface plankton taken during 7 upwelling episodes (Table 2) and 10 downwelling episodes (Table 3).

More prey were consumed during the downwelling episodes (e.g., $\bar{x}$ no. prey taken = 110.8, vs. 20.1 during upwelling episodes). Thaliacians (Fig. 6) were the primary food during the upwelling season, but all were taken during downwelling episodes—the only times when the guts were packed with food. These relatively large, gelatinous zooplankters did not occur either in the plankton or in the diet of *S. mystinus* during upwelling episodes.

TABLE 2.—*Continued.*

| Food organism | | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 8 | CAPRELLIDEA (0.54) | **10** | **5** | **1.08** | **0.1** | **6** | **14** | **2.25** | **0.4** |
| | *Metacaprella kennerlyi* | 10 | 5 | 1.08 | 0.1 | — | 0 | 0.00 | 0.0 |
| | Others | — | 0 | 0.00 | 0.0 | 6 | 14 | 2.25 | 0.4 |
| 9 | CHAETOGNATHA (0.09) | **23** | **3** | **0.03** | **1.0** | **3–12** | **57** | **20.80** | **2.1** |
| | Undetermined species | 23 | 3 | 0.03 | 1.0 | 3–12 | 57 | 20.80 | 2.1 |
| 10 | FISHES (0.02) | **12** | **3** | **0.05** | **0.1** | **2–14** | **57** | **14.92** | **1.1** |
| | Larvae | 12 | 3 | 0.05 | 0.1 | 2–14 | 57 | 14.92 | 1.1 |
| OTHER CATEGORIES | | | | | | | | | |
| Polychaeta | | — | 0 | 0.00 | 0.0 | <1–12 | 86 | 74.83 | 1.4 |
| Molluscan larvae | | — | 0 | 0.00 | 0.0 | <1–1 | 57 | 149.92 | 1.7 |
| Pelagic gastropoda | | — | 0 | 0.00 | 0.0 | 1–5 | 29 | 2.32 | 8.6 |
| Cladocera | | — | 0 | 0.00 | 0.0 | 1 | 29 | 64.28 | 0.7 |
| Harpacticoida | | — | 0 | 0.00 | 0.0 | 1–2 | 1 | 54.77 | 0.7 |
| Cyclopoidea | | — | 0 | 0.00 | 0.0 | 1 | 71 | 75.08 | 0.9 |
| Cirripedean larvae | | — | 0 | 0.00 | 0.0 | <1–1 | 1 | 1850.92 | 15.0 |
| Reptantian larvae | | — | 0 | 0.00 | 0.0 | <1–2 | 86 | 134.48 | 1.9 |
| Natantian larvae | | — | 0 | 0.00 | 0.0 | 2–3 | 43 | 72.00 | 1.4 |
| Larvacea | | — | 0 | 0.00 | 0.0 | 3–8 | 43 | 53.48 | 1.1 |
| Eggs, undetermined | | — | 0 | 0.00 | 0.0 | <1 | 43 | 3024.00 | 9.7 |
| Eggs, fish | | — | 0 | 0.00 | 0.0 | <1–2 | 71 | 312.68 | 1.7 |
| UNIDENTIFIABLE MATERIAL[8] | | — | — | — | 15.9 | — | — | — | — |

No. fish examined: 51
224–336, $\bar{x}$ = 284.3 mm SL
No. empty = 13
$\bar{x}$ no. prey: individuals = 20.13
taxa = 2.03

No. plankton collections: 7
$\bar{x}$ no. zooplankters: 4940.57

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[1] Value is estimated mean number per 100 m$^3$ of water, based on water filtered (54.8 m$^3$) during the 5-min collection.

[2] NR = not recorded. The enumeration was either omitted or unfeasible.

[3] *Velella velella* floats on the water's surface, where it was not effectively sampled by our net.

[4] Most mysids sampled were *Acanthomysis sculpta*.

[5] Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata* (Fig. 5), which were avoided by us during plankton collections because they would have made collections unmanageable.

[6] According to Kathleen Conlan (National Museum of Canada, P.O. Box 3443, Station D, Ottawa, Canada K1P 6P4, pers. commun. 26 May 1987), *Jassa falcata* does not occur in California, and forms along the coast considered to be this species (including the form(s) referred to here) are undescribed.

[7] Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.

[8] Foods digested beyond recognition.

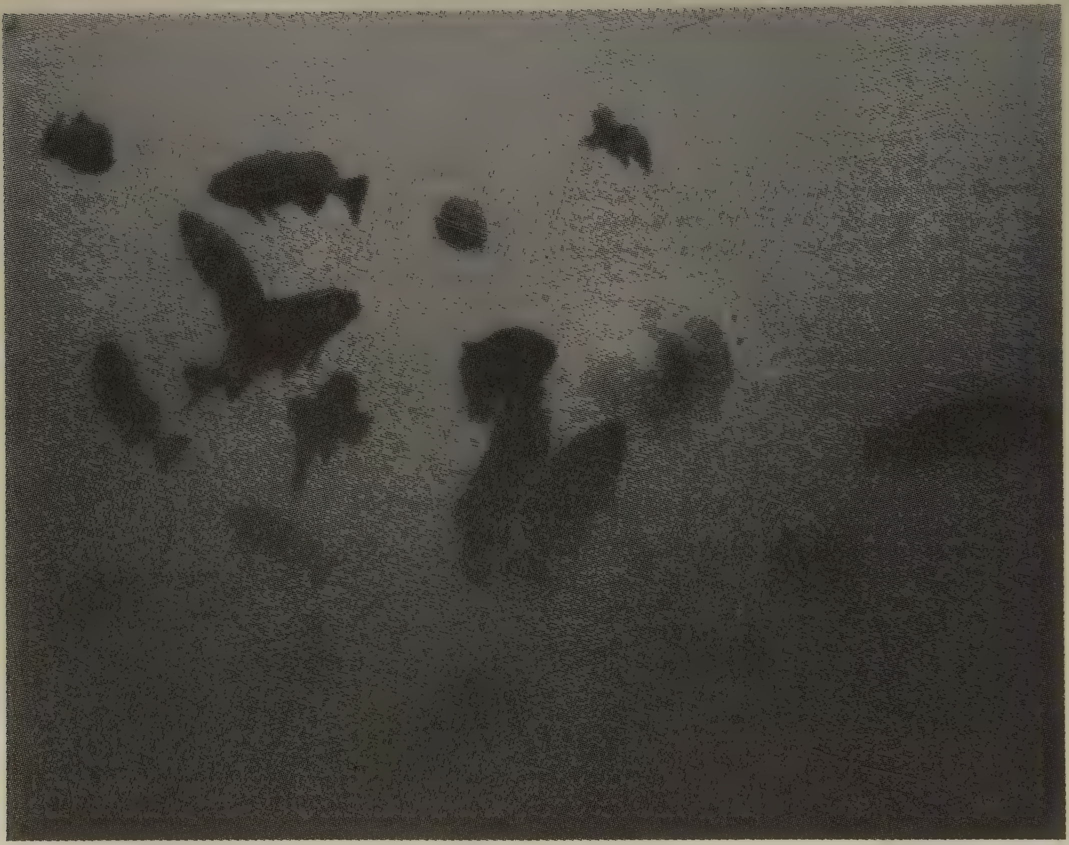

FIGURE 5.—Adult *Sebastes mystinus* feeding on a scyphozoan, *Cyanea capillata*.

TABLE 3.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of the upwelling season. $n$ = 10.

| Food organism | | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 1 | **THALIACEA (124990.86)** | **1–10** | **47** | **76.20** | **34.9** | **3–45** | **30** | **130.70** | **8.9** |
| | Undetermined species | 1–10 | 47 | 76.20 | 34.9 | 3–45 | 30 | 130.70 | 8.9 |
| 2 | **PLANTS (2030.40)** | **NR**[2] | **54** | **NR** | **37.6** | **NR** | **NR** | **NR** | **NR** |
| | *Nereocystis* sori | NR | 18 | NR | 9.7 | NR | NR | NR | NR |
| | *Porphyra* sp. | NR | 22 | NR | 11.5 | NR | NR | NR | NR |
| | *Smithora naidum* | NR | 15 | NR | 5.5 | NR | NR | NR | NR |
| | Others | NR | 28 | NR | 10.9 | NR | NR | NR | NR |

TABLE 3.—*Continued.*

| Food organism | | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 3 | CALANOIDA (778.78) | **3–6** | **20** | **16.93** | **2.3** | **<1–8** | **100** | **5557.10** | **31.9** |
| | Nauplii | — | 0 | 0.00 | 0.0 | <1–1 | 50 | 594.00 | 1.8 |
| | *Acartia* spp. | — | 0 | 0.00 | 0.0 | 1–2 | 1 | 1121.00 | 4.6 |
| | *Calanus pacificus* | — | 0 | 0.00 | 0.0 | 2–5 | 70 | 105.84 | 2.4 |
| | *Eucalanus californicus* | 4–6 | 20 | 16.92 | 2.3 | 1–8 | 70 | 796.68 | 14.6 |
| | *Rhincalanus nasutus* | — | 0 | 0.00 | 0.0 | 5–6 | 10 | 92.88 | 2.7 |
| | Others[3] | 3 | 1 | 0.01 | <0.1 | <1–3 | 1 | 2846.70 | 5.8 |
| 4 | HYPERIIDEA (405.13) | **2–13** | **49** | **6.36** | **1.3** | **1–7** | **60** | **17.10** | **0.6** |
| | *Hyperoche medusarum* | 2–6 | 5 | 0.38 | 0.1 | 1–7 | 20 | 9.72 | 0.3 |
| | *Vibilia* spp. | 5 | 24 | 4.35 | 0.7 | — | 0 | 0 | 0 |
| | Others | 2–13 | 23 | 1.63 | 0.5 | 1–3 | 40 | 7.38 | 0.3 |
| 5 | PELAGIC GASTROPODA (334.66) | **1–20** | **16** | **5.81** | **3.6** | **1–18** | **20** | **37.44** | **1.1** |
| | Heteropoda | | | | | | | | |
| | *Caranaria japonica* | 10–20 | 8 | 2.35 | 2.0 | — | 0 | 0.00 | 0.0 |
| | Pteropoda | | | | | | | | |
| | *Corolla spectabilis* | 10–15 | 11 | 3.45 | 1.6 | 15–18 | 10 | 4.32 | 0.8 |
| | *Limacina helicina* | 3 | 1 | 0.01 | <0.1 | 1–2 | 20 | 33.12 | 0.3 |
| | Others | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| 6 | PELAGIC HYDROZOA (318.24) | **2–35** | **30** | **1.56** | **6.8** | **1–20** | **70** | **240.66** | **8.8** |
| | Hydromedusae | | | | | | | | |
| | *Eutonina indicans* | — | 0 | 0.00 | 0.0 | 10–20 | 10 | 0.54 | 0.3 |
| | Others | — | 0 | 0.00 | 0.0 | 1–5 | 50 | 187.56 | 5.8 |
| | Syphonophora | | | | | | | | |
| | *Muggiaea atlantica* | 8–9 | 5 | 0.27 | 0.2 | 6–9 | 10 | 2.88 | 0.6 |
| | *Stephanomia bijuga* | NR | 5 | 0.31 | 0.2 | — | 0 | 0.00 | 0.0 |
| | Others | 2–16 | 14 | 0.51 | 2.7 | 2–6 | 20 | 49.68 | 2.1 |
| | Chondrophora | | | | | | | | |
| | *Velella velella*[4] | 25–35 | 7 | 0.47 | 3.7 | NA[4] | NA | NA | NA |
| 7 | LARVACEA (1.12) | **2–7** | **8** | **0.70** | **0.2** | **2–6** | **70** | **142.74** | **2.2** |
| | Undetermined | 2–7 | 8 | 0.70 | 0.2 | 2–6 | 70 | 142.74 | 2.2 |
| 8 | POLYCHAETA (0.87) | **4–25** | **19** | **0.46** | **0.1** | **<1–7** | **70** | **103.50** | **0.7** |
| | Larvae | — | 0 | 0.00 | 0.0 | <1–4 | 70 | 90.36 | 0.3 |
| | Postlarvae | 4–25 | 19 | 0.46 | 0.1 | 7 | 10 | 13.14 | 0.4 |
| 9 | FISHES (0.73) | **8–45** | **4** | **0.14** | **1.3** | **2–11** | **50** | **4.50** | **0.4** |
| | Larvae | 8–45 | 4 | 0.14 | 1.3 | 2–11 | 50 | 4.50 | 0.4 |
| 10 | SCYPHOZOA (0.02) | **NR** | **3** | **0.01** | **0.5** | **NR** | **NR** | **NR** | **NR** |
| | Fragments | NR | 3 | 0.01 | 0.5 | NR | NR | NR | NR |
| OTHER CATEGORIES | | | | | | | | | |
| | Molluscan larvae | NR | 1 | 0.01 | <0.1 | <<1–<1 | 70 | 631.08 | 4.9 |
| | Cladocera | — | 0 | 0.00 | 0.0 | <<1–<1 | 40 | 115.92 | 1.7 |
| | Harpacticoida | NR | 3 | 0.03 | NR | <1–2 | 70 | 55.25 | 1.1 |
| | Cirripedean larvae | — | 0 | 0.00 | 0.0 | <1–2 | 100 | 1372.44 | 11.8 |
| | Gammaridea | 1–8 | 12 | 0.32 | 0.5 | <1–3 | 90 | 12.24 | 0.6 |
| | Euphausiacea | 2–12 | 9 | 0.11 | 0.7 | <1–11 | 60 | 229.86 | 1.0 |
| | Reptantian larvae | — | 0 | 0.00 | 0.0 | <1–3 | 70 | 119.52 | 2.1 |
| | Natantian larvae | — | 0 | 0.00 | 0.0 | 1–6 | 60 | 43.20 | 0.7 |
| | Chaetognatha | — | 0 | 0.00 | 0.0 | 6–18 | 50 | 18.54 | 1.2 |
| | Eggs, undetermined | NR | 12 | 0.74 | 0.3 | <<1–<1 | 50 | 2921.40 | 5.0 |
| | Eggs, fish | — | 0 | 0.00 | 0.0 | <1–2 | 60 | 48.96 | 0.9 |
| UNIDENTIFIABLE MATERIAL[5] | | — | — | — | 11.0 | — | — | — | — |

No. fish examined: 85
204–335, $\bar{x}$ = 266.2 mm SL
No. empty = 8
$\bar{x}$ no. prey: individuals = 110.84
taxa = 3.35

No. plankton collections: 10
$\bar{x}$ no. zooplankters: 6622.50.

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[1] Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.

[2] NR = not recorded. The enumeration was either omitted or unfeasible.

[3] Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.

[4] *Velella velella* floats on the water's surface, where it was not effectively sampled by our net.

[5] Foods digested beyond recognition.

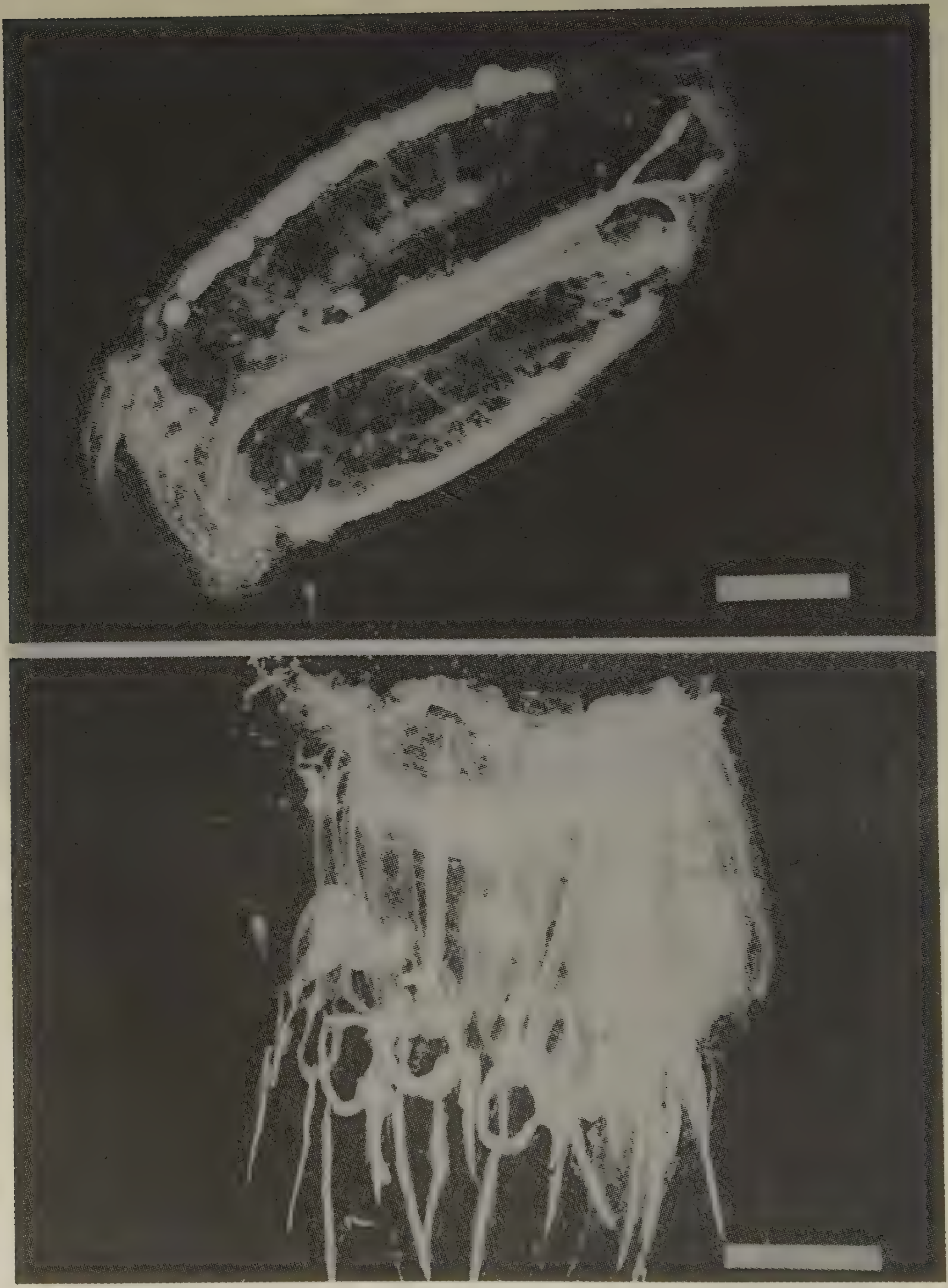

FIGURE 6.—Thaliacean, *Cyclosalpa bakeri*, off Mendocino. Solitary individual (upper) and aggregate of individuals (below). Scale indicator = 1 cm.

Plant material ranked as the top food-category during upwelling episodes (Table 2) and as the second-ranked food during downwelling episodes (Table 3). In both cases, certain algae dominated the diet on days when offshore zooplankters were in short supply during the latter part of the upwelling season (upwelling episodes on 8 August 1978, 12 June 1979, and 17 June 1981; downwelling episodes on 24 July 1979 and 27 August 1979; see Table 1). Algae were not taken earlier in the season, however. Thus, while the six individuals collected during a plankton-poor upwelling episode of 8 August 1978 (Table 1) were full of algae (90% of gut contents) and epibenthic crustaceans (10%), all eight collected during a plankton-poor upwelling episode of 9 April 1981 (Table 1) were empty. Similarly, the occurrence of algae in the diet during downwelling episodes (Table 3) is based mostly on 20 adults collected during two days (24 and 27 August 1979) when environmental conditions indicated downwelling but an absence of offshore zooplankters was noted (Table 1). There was no indication of plants being ingested for epiphytic animals.

Of the wide variety of plant materials in the diet, only the three most frequently ingested forms appeared to some extent digested. These were the sori of *N. leutkeana*, *Porphyra nereocystis* (an epiphyte on *N. leutkeana*), and *Smithora naidum* (an epiphyte on certain seagrasses). The sori of *N. leutkeana* developed as variably sized areas (typically about 50–150 mm long) in fronds near the water's surface. They dropped from the fronds when mature, and we saw several ingested by *S. mystinus* as they drifted toward the bottom. Sori recovered from the intestines of *S. mystinus* were more translucent than sori from the stomach, but comparison under magnification of sectioned material from both regions of the gut (Fig. 7) indicated that only zoospores were digested. Ingested fragments of *P. nereocystis* and *S. naidum*, both species having monostromatic thalli, ranged from intact, but flaccid and blanched, to disintegrating. Ingested *S. naidum* often were attached to pieces of *Zostera marina* or *Phyllospadix torreyi*, but these seagrasses never evidenced digestion. Nor did other plant forms present among the gut contents appear to be digested, including *D. ligulata* and *N. leutkeana* (vegetative tissue), along with various unidentified phaeophytes and rhodophytes. Thus, plants contributed less food than is indicated by the tables and histograms, where their rank is inflated by undigested materials.

Zooplankters taken during upwelling episodes differed from early to late in the season, whereas those taken during downwelling episodes remained much the same throughout (as listed in Table 3). Thus, of the food categories listed for the upwelling condition (Table 2), pelagic hydrozoans, mysids, and scyphozoans were taken only during the spring, whereas euphausiids and caprellids were taken only in summer. The only notable departure from the downwelling condition depicted in Table 3 occurred on 24 April 1979 (Table 1), when conditions were at the time judged to be mixed. Upwelling had been unusually weak during the first month of that upwelling season, and there was no wind at the time of sampling. The sea was calm and, at 10°C, warm for April. Although these conditions usually indicate downwelling (which is why the data are assigned to that category), we neither collected nor saw organisms typical of downwelling conditions. Furthermore, of the nine adult *S. mystinus* (224–313, $\bar{x} = 277.7$ mm SL) collected, eight (89%) were empty. The ninth contained one sorus from *N. leutkeana* (an unusually large number of *N. leutkeana* had persisted through the previous winter, which had been exceptionally mild) and also organisms not seen or collected by us in the environment at the time: two *Corolla spectabilis* (a pelagic gastropod typical of downwelling conditions) and six *Velella velella* (a pelagic hydrozoan typical of upwelling conditions). The latter float on the water's surface (Fig. 8), and often we saw adult *S. mystinus* break the surface to feed on them.

## The Downwelling Season

Between late August and mid-September it became evident that transition to the downwelling season was under way. Winds had become light and variable (but generally remained either northerly or southerly), and for a growing number of days at a time, the water was notably blue and transparent. Records of sea temperatures and wind for the 1980–81 downwelling season illustrate how occurrences of downwelling and upwelling related to prevailing wind during that period (Fig. 9).

### Habitat Conditions

The downwelling season developed with less wind from the north and more wind from the south, but either way with winds that tended to be light, so that relatively tranquil conditions prevailed. Flowing into the nearshore habitat with offshore surface waters was a rich supply of relatively large, mostly gelatinous zooplankters that were major prey of *S.*

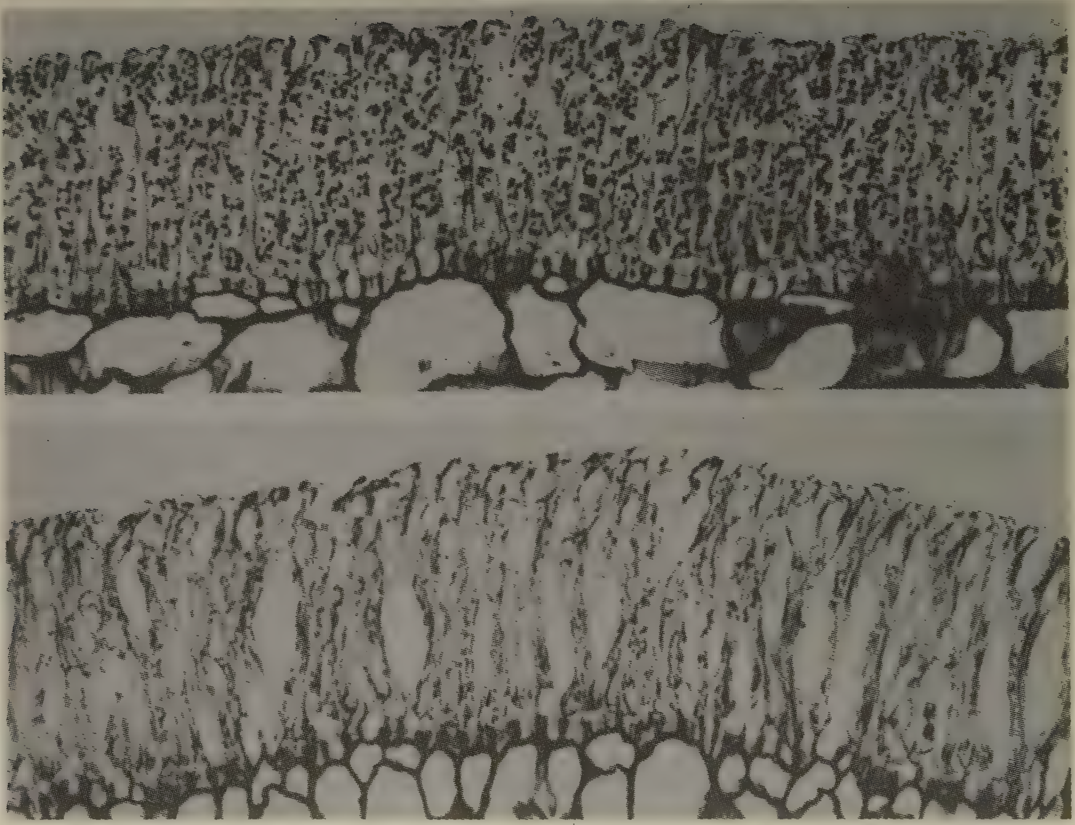

FIGURE 7.—Sections through surface region of sori (stained with hematoxylin) from gut of *Sebastes mystinus*. Upper section is from the stomach, lower is from the intestine. Granular objects in upper section but largely absent in lower section are zoospores in zoosporangia.

*mystinus*. But, whereas the predominant of such forms during spring and summer usually were thaliaceans, during the fall they were usually ctenophores (Fig. 10), pelagic hydrozoans—mostly siphonophores (Fig. 11), and hydromedusae. The pelagic hydrozoan *Velella velella*, which had been prominent during the upwelling season, was not seen. Pelagic gastropods (Fig. 12), pteropods at least, also were more abundant during fall downwelling. On the other hand, these waters were poor in the pelagic diatoms that had bloomed periodically during spring and summer. Furthermore, the nearshore habitat had by this time lost much of its benthos. Many of the more insecurely anchored *Nereocystis* plants, for example, had been carried away by strong wave surge that frequently swept through the nearshore habitat even during relatively tranquil periods. Although the loss of these plants greatly increased interplant distances, *Nereocystis* beds remained dominant features. This was because the plants still in place continued to grow, to produce sori, and to thicken the surface canopy. Probably at least partly because the canopy's increased thickness blocked sunlight from the seafloor below, the algal understory, *Desmarestia lingulata* in particular, was greatly reduced. Similarly, many benthic animals that proliferated during the previous upwelling season had become scarce, including the amphipods and mysids noted above to be declining during late summer.

As the downwelling season progressed through fall toward winter, there were major transformations of the nearshore habitat that, to at least some extent, resulted from southwesterly storms. The

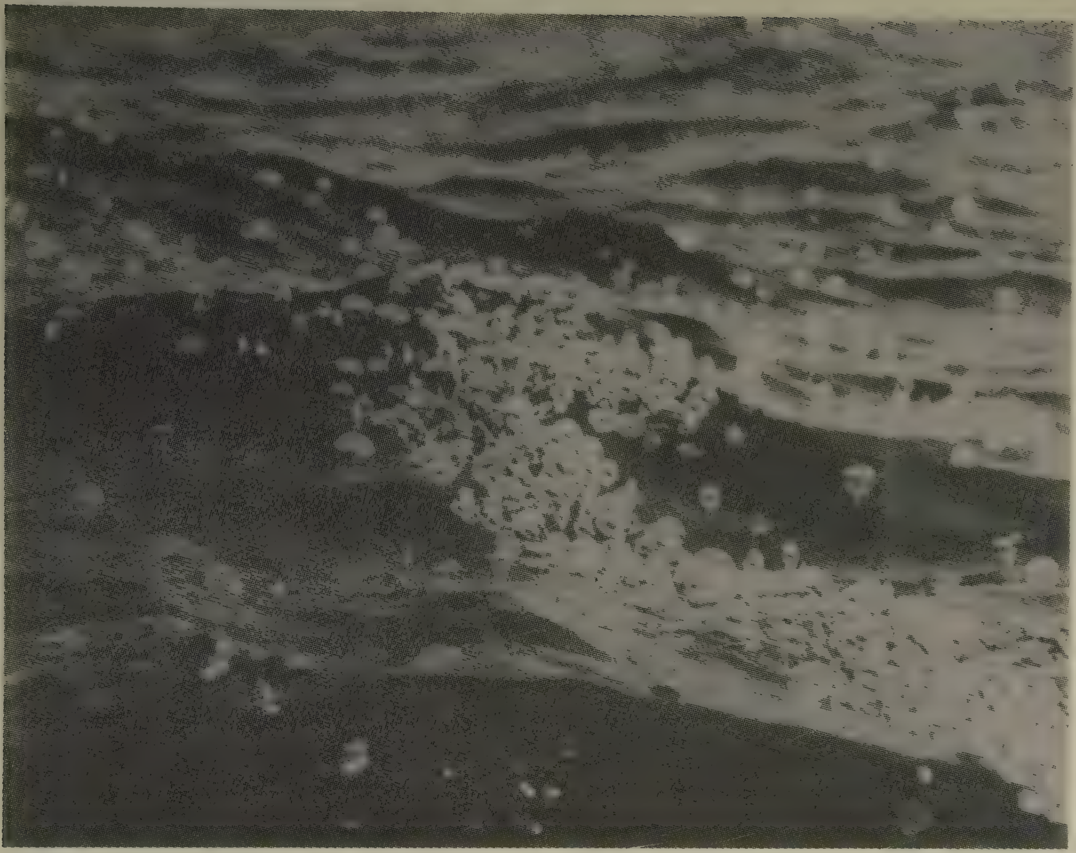

FIGURE 8.—*Velella velella* being driven shoreward by a northwest wind off the coast of northern California.

major effects of storms on the nearshore habitats came from 1) physical force of waves and surge, and 2) suspended sediments carried by coastal runoff into the nearshore habitats after heavy rains. The first of these was the more apparent, at least in exposed locations where often many of the benthic algae and sessile invertebrates were swept away. This force, intensified when the water carried abrasive sediments, swept away most of the *Nereocystis*, although some plants survived the winter in sheltered places where they continued to produce sori. Suspended sediments had their most obvious effects in locations sheltered from water movement, where they frequently settled to blanket the benthos. Probably a more profound effect of materials in suspension, however, was reduced transparency of the water that limited the amount of light (already at low levels owing to the shorter days and low sun angle) reaching phototrophic organisms.

As a general result of these, and probably other forces in combination, the nearshore habitat appeared relatively barren during the latter stages of the downwelling season. That storms were a major factor in reducing the vitality of this habitat was apparent during the relatively mild winter of 1978–79, when the effects described above were reduced. That was the only year, for example, when mysids were noted to be conspicuous in the nearshore habitat throughout the winter.

### Feeding Conditions

The diet of *S. mystinus* relative to foods available during the downwelling season was assessed during 10 days of sampling under downwelling condi-

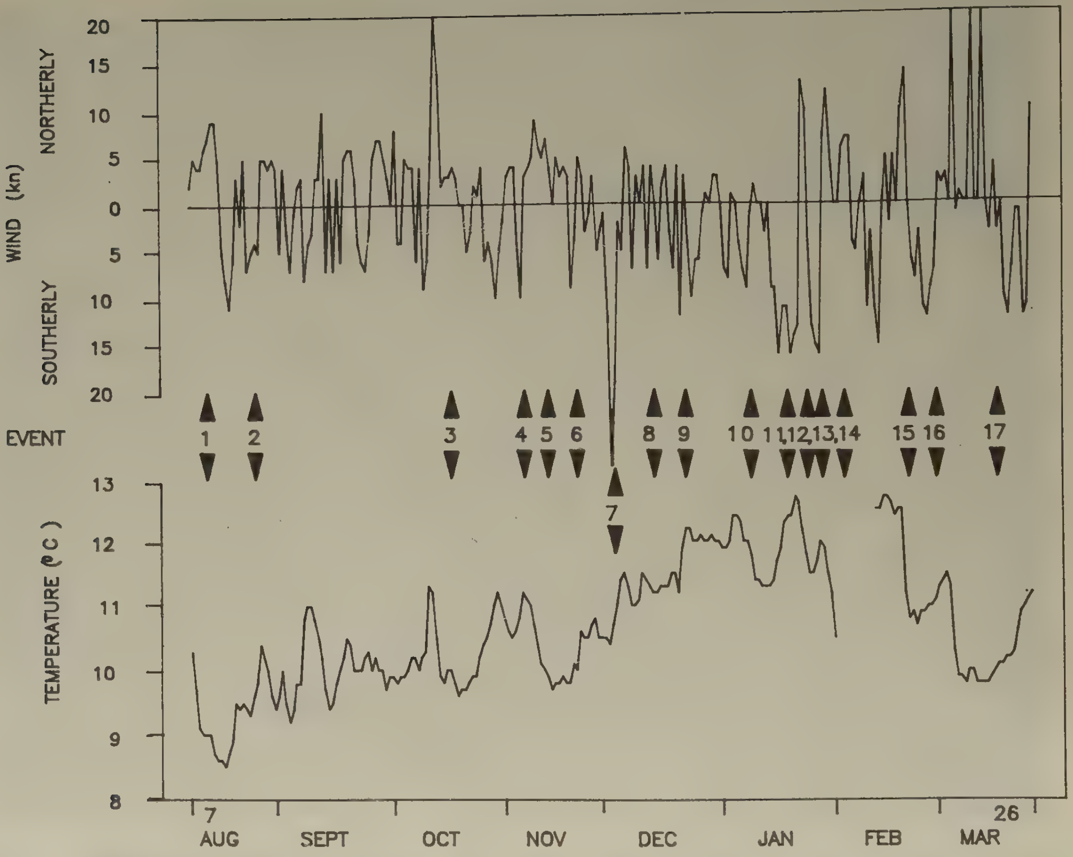

FIGURE 9.—Sea temperatures and wind off Mendocino during the 1980–81 downwelling season. See capture of Figure 4 and text for methods used in obtaining and plotting the data.

Event 1—Sea temperature fell to 8.5°C on 16 August after 9 consecutive days of 7–10 K northerlies, producing the last episode of strong upwelling during the 1980 upwelling season.

Event 2—Sea temperature rose to 10.4°C on 26 August after southerlies of 5–12 K on 9 of the preceding 11 days. Then began a 6-wk transition to the downwelling season, during which 1–4 day periods of 2–10 K northerlies, with slightly lowered sea temperatures, alternated with 1–4 day periods of southerlies, with slightly elevated temperatures.

Event 3—The last bit of upwelling before the season's first major downwelling episode began on 14 October with 7 consecutive days of northerlies—20 K during the first 2, 4–8 K during the next 5.

Event 4—Sea temperatures rose to 11.2°C on 7 November after 16 straight days of 2–12 K southerlies or weak (2–5 K) northerlies.

Event 5—Sea temperatures fell to 9.7°C during a major cooling that coincided with 8 days of 3–9 K northerlies (with gusts to 20 K) from 8 to 15 November.

Event 6—On 21 November the wind shifted to the south, with gusts to 20K, and sea temperatures began rising.

Event 7—A 3-day storm (1–3 December) with 20–30 K southerlies (and rain) briefly accelerated the rise in temperature.

Event 8—The warming trend was briefly interrupted by several 1–3 day periods of 4–10 K northerlies.

Event 9—By 22 December sea temperatures had risen to levels above 12°C that characterized the 1980–81 downwelling season. Although southerlies predominated over the next 3 weeks, on some days reaching 25 K (e.g., on 25 December), there were no further large increases in temperature.

Event 10—Sea temperatures anomalously fell during the first 2 weeks of January, even though winds during that period were mostly southerlies of up to 10 K.

Event 11—An 8-day storm (15–22 January) with 12–20 K southerlies (and rain) resulted in sea temperatures rising to 12.7°C—the warmest of the year (equaled 3 weeks later).

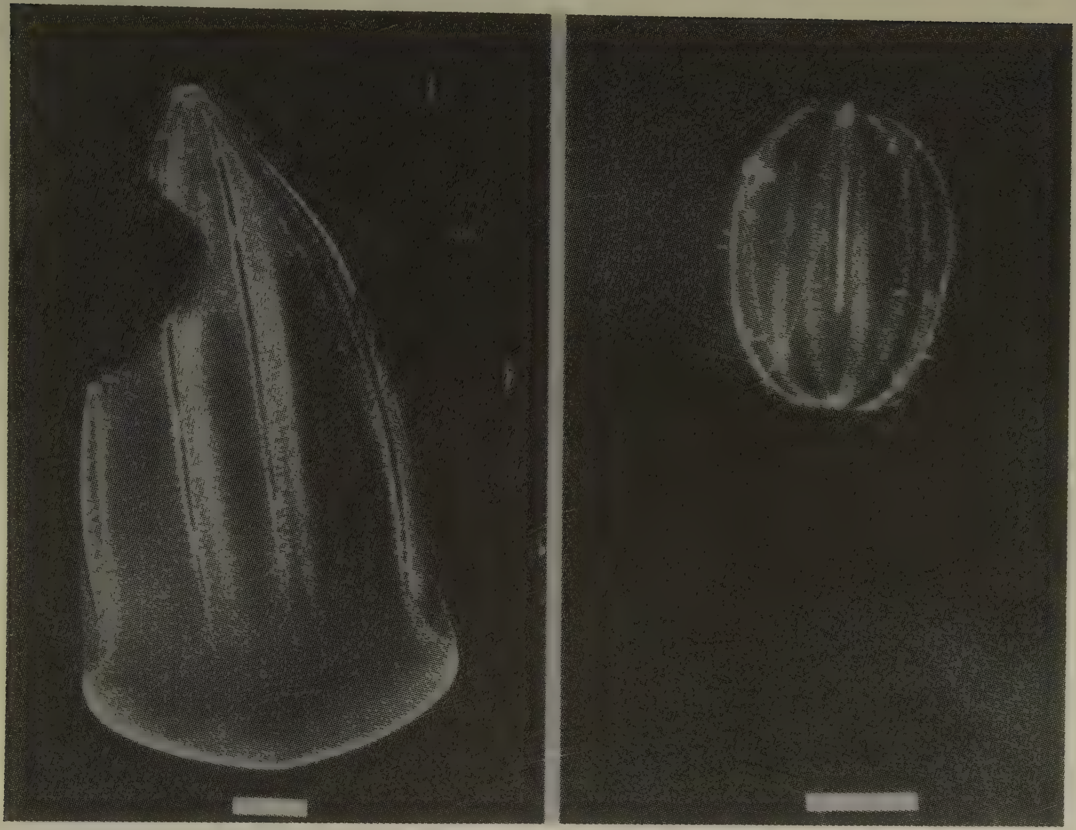

FIGURE 10.—Ctenophores off Mendocino. *Beroe forskali* (left), missing piece probably taken by planktivore, and *Pleurobrachia bachei* (right). Scale indicator = 1 cm.

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EVENT 12—The process abruptly reversed with a shift to northerlies that gusted to 30 K for 2 days, and sea temperature fell to 11.5°C on 25 January.

EVENT 13—In another abrupt reversal, 3 days (27–29 January) of 15–25 K southerlies (with rain) resulted in sea temperature rising to 12°C.

EVENT 14—Reversing again, northerlies of 12–20 K on 30–31 January drove sea temperatures down to 10.5°C, at which point (1 February) the thermograph malfunctioned. Southerlies predominated while the thermograph was inoperative, and when it was reinstalled on 11 February, rising sea temperature 2 days later (13 February) equaled the season high of 12.5°C. But when northerlies returned the next day the downwelling season began its decline.

EVENT 15—Two days of 20–25 K northerlies (19–20 February) resulted in the season's largest 24-h change in sea temperatures.

EVENT 16—Sea temperature rose to 11.5°C on 3 March following 8 consecutive days of 8–15 K southerlies (with rain), or weak northerlies (to 6 K). An abrupt shift followed, as 2 days of 15–25 K northerlies (4–5 March) resulted in the season's second largest 24-h change in sea temperature—the first time since November that sea temperature had fallen below 10°C.

EVENT 17—After a week of light variable winds, during which sea temperatures remained essentially unchanged at about 9.8°C, southerlies increased to 15–20 K (on 15 March) and sea temperatures began rising to begin the final downwelling episode of the 1980–81 downwelling season (which was followed by the abrupt reversal that marked the beginning of the 1981 upwelling season, see Figure 4).

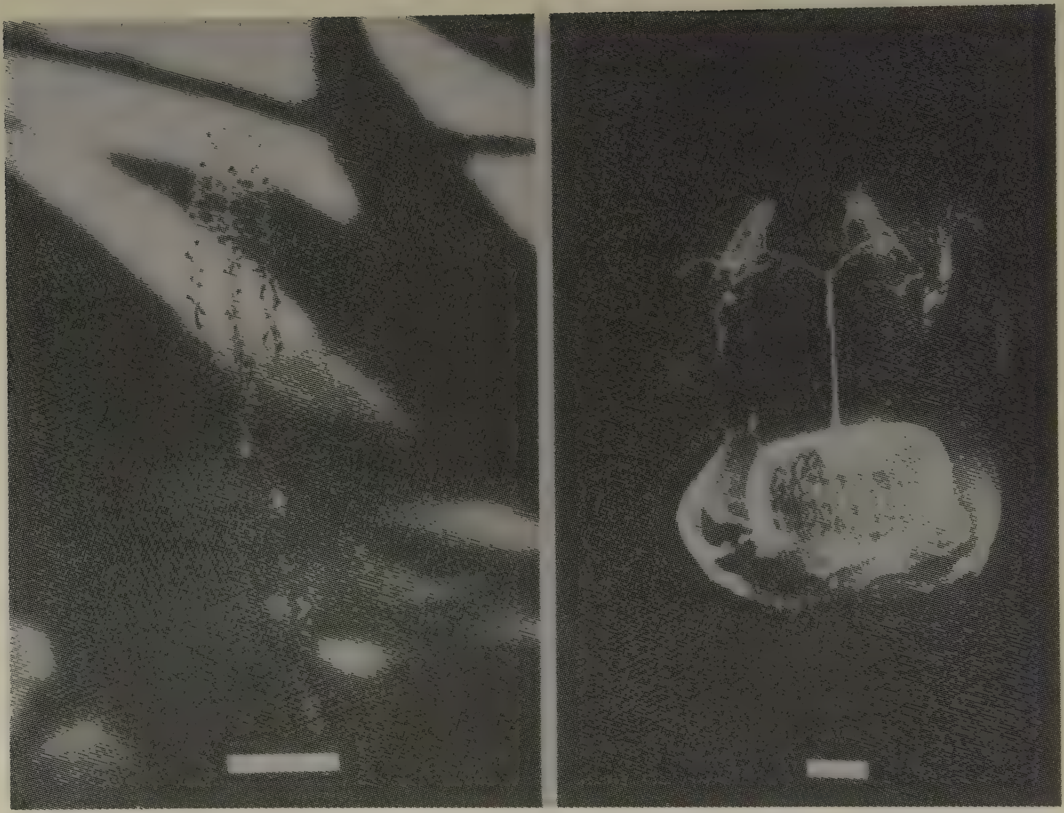

FIGURE 11.—Siphonophores off Mendocino. The physonect *Stephanomia bijuga* (left), and the calycophore *Praya dubia* (right). Scale indicator = 1 cm.

tions, but because fall and winter were so different, we consider them separately. We did not observe upwelling conditions during this period.

The major foods during six days of fall downwelling, based on the ranking indices (Table 4), were pelagic hydrozoans, specifically siphonophores, but vegetation comprised a larger part of the total diet volume. Virtually all plant materials taken at these times, however, were sori of *N. leutkeana*. As was true during the upwelling season, there tended to be more vegetation in the diet when there were fewer of the larger gelatinous zooplankters in the water column. For example, during the sampling session of 18 October 1978 (Table 1), when the surface plankton-collections took 400 siphonophores and ctenophores, only 1 of the 9 fish collected had consumed plant material (one sorus of *N. leutkeana*). On the other hand, during the sampling session of 16 October 1979 (Table 1), when the surface plankton-collection took only 30 siphonophores and ctenophores, 10 of 13 fish collected had consumed vegetation ($\bar{x}$ diet volume = 80%, virtually all of it sori of *N. leutkeana*; number taken = 1–21, $\bar{x}$ = 9.0), and two others were empty.

Our assessment of the diet and concurrent composition of the plankton during winter downwelling is limited to four days of sampling (Table 5). Data from these collections are combined for consistency

FIGURE 12.—Pelagic gastropods off Mendocino. The heteropod *Caranaria japonica* (upper), and the pteropod *Corolla spectabilis* (lower). Scale indicator = 1 cm. Often in areas where blue rockfish are feeding many of the *C. spectabilis* present have lost the bulbous central part of their body (pseudoconch and viscera).

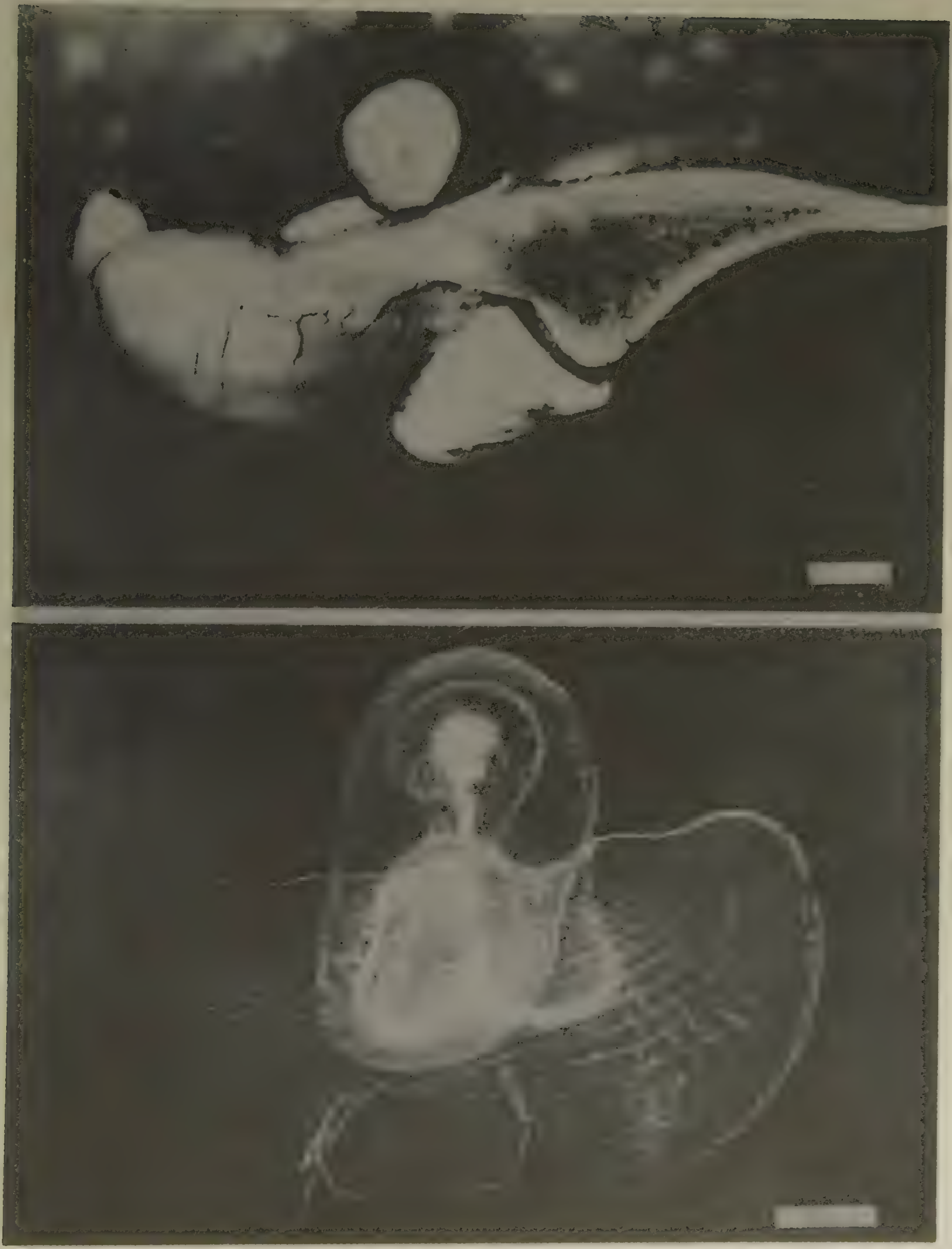

TABLE 4.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of fall. $n = 6$.

| Food organism | | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 1 | PELAGIC HYDROZOA (10455.98) | **2–15** | **46** | **18.04** | **12.5** | **1–25** | **83** | **1747.12** | **26.5** |
| | Hydromedusae | | | | | | | | |
| | *Eutonina indicans* | 18 | 1 | 0.03 | <0.1 | 18–25 | 33 | 1516.81 | 14.7 |
| | Others | 15 | 4 | 0.02 | <0.1 | <1–20 | 33 | 26.10 | 0.2 |
| | Syphonophora | | | | | | | | |
| | *Muggiaea atlantica* | 6–15 | 10 | 0.34 | 0.7 | 5–12 | 67 | 15.83 | 2.0 |
| | *Stephanomia bijuga* | 10 | 17 | 1.33 | 0.8 | 10 | 17 | 2.39 | 0.3 |
| | Others | 2–15 | 31 | 16.32 | 10.9 | 1–8 | 4 | 185.99 | 9.3 |
| | Chondrophora | | | | | | | | |
| | *Velella velella*[2] | — | 0 | 0.00 | 0.0 | NA[2] | NA | NA | NR |
| 2 | PLANTS (4123.00) | **NR[3]** | **54** | **2.06** | **37.1** | **NR** | **NR** | **NR** | **NR** |
| | *Nereocystis* sori | NR | 51 | 1.94 | 35.6 | NR | NR | NR | NR |
| | *Porphyra* sp. | NR | 2 | NR | 0.2 | NR | NR | NR | NR |
| | *Smithora naidum* | NR | 6 | 0.06 | <0.1 | NR | NR | NR | NR |
| | Others | NR | 6 | 0.06 | 1.3 | NR | NR | NR | NR |
| 3 | CTENOPHORA (1742.66) | **3–15** | **33** | **5.74** | **9.2** | **<1–10** | **0.67** | **295.79** | **5.4** |
| | *Pleurobrachia bachei* | 3–15 | 31 | 5.73 | 9.2 | <1–10 | 50 | 288.59 | 5.2 |
| | Others | 12 | 1 | 0.01 | <0.1 | 3 | 17 | 7.20 | 0.2 |
| 4 | PELAGIC GASTROPODA (554.00) | **2–160** | **25** | **3.20** | **6.8** | **<1–45** | **100** | **187.82** | **8.4** |
| | Heteropoda | | | | | | | | |
| | *Caranaria japonica* | 12–160 | 15 | 0.33 | 2.1 | 30–45 | 17 | 1.21 | 0.7 |
| | Pteropoda | | | | | | | | |
| | *Corolla spectabilis* | 5–22 | 16 | 2.69 | 4.7 | 2–20 | 50 | 72.90 | 7.5 |
| | *Limacina helicina* | 2 | 1 | 0.18 | <0.1 | 1–3 | 17 | 109.80 | 0.2 |
| | Others | — | 0 | 0.00 | 0.0 | <1–3 | 17 | 3.91 | <0.1 |
| 5 | SCYPHOZOA (89.96) | **10–35** | **18** | **0.51** | **9.8** | **NA** | **NA** | **NA** | **NA** |
| | Fragments | 10–35 | 18 | 0.51 | 9.8 | NA | NA | NA | NA |
| 6 | THALIACEA (31.97) | **5–29** | **16** | **0.54** | **3.7** | **2–5** | **17** | **3.01** | **NR** |
| | Undetermined species | 5–29 | 16 | 0.54 | 3.7 | 2–5 | 17 | 3.01 | NR |
| 7 | EUPHAUSIACEA (22.93) | **4–10** | **21** | **0.78** | **1.4** | **<1–9** | **67** | **162.90** | **2.2** |
| | Larvae | 4 | 1 | 0.01 | <0.1 | 4 | 50 | 129.01 | 1.2 |
| | *Thysanoessa* spp. | 4–10 | 19 | 0.74 | 1.4 | 5–9 | 33 | 33.89 | 1.0 |
| | Others | 8 | 1 | 0.03 | <0.1 | — | 0 | 0.00 | 0.0 |

with the other tables and figures, but the combinations obscure the great variation in feeding conditions at this time of year. For example, taxa of the major food categories listed in Table 5 were numerous in the diet and plankton only during the two sampling sessions in February and March of 1979. Of the 14 fish collected at those times, all but one was well fed ($\bar{x}$ no. prey = 26.7), with the exception being a pregnant female whose gut was empty. Thaliaceans dominated on these occasions, both in the diet and in the plankton, and hyperiid amphipods, *Vibilia* spp. (which are parasites of thaliaceans (Laval 1980)), were similarly abundant. In contrast, the collecting session of January 1980 indicated there were more zooplankters in the water column, but that they were exceptionally small. The plankton collection took 1,488 zooplankters (compared with 109 and 715 in the two 1979 collections), but only 2% were of species that occurred as large as 2 mm (compared with 86% in 1979). That these small zooplankters were unsuitable as prey of adult *S. mystinus* is implicit in the fact that of 16 fish collected, only 3 contained food—all of it the alga *Porphyra* sp. (The other 13 represented 76% of all fish with empty guts in the winter collections.) Significantly, of the taxa identified as food of adult *S. mystinus* during the winter (Table 5), only one, the calanoid *Calanus pacificus*, was represented in the January 1980 plankton collection. Conditions were intermediate during the sampling session of January 1981, when some of the listed food taxa occurred in both diet and plankton (though in reduced numbers) and five of eight fish sampled contained food.

TABLE 4.—*Continued.*

| Food organism | | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 8 | CALANOIDA (14.32) | **2–7** | **22** | **0.93** | **0.7** | **<1–7** | **100** | **9528.11** | **28.3** |
| | Nauplii | — | 0 | 0.00 | 0.0 | <1–1 | 33 | 68.99 | <0.1 |
| | *Acartia* spp. | — | 0 | 0.00 | 0.0 | <1–1 | 83 | 1751.42 | 4.3 |
| | *Calanus pacificus* | 3 | 6 | 0.13 | <0.1 | <1–4 | 83 | 4609.21 | 15.8 |
| | *Eucalanus californicus* | 4–7 | 15 | 0.67 | 0.7 | 2–7 | 100 | 255.39 | 1.2 |
| | *Rhincalanus nasutus* | 4 | 4 | 0.06 | <0.1 | — | 0 | 0.00 | 0.0 |
| | Others[4] | 2–3 | 3 | 0.07 | <0.1 | <1–3 | 100 | 2843.10 | 7.0 |
| 9 | HYPERIIDEA (8.28) | **1–8** | **24** | **1.15** | **0.4** | **1–7** | **83** | **292.19** | **0.4** |
| | *Hyperoche medusarum* | 2 | 3 | 0.16 | 0.1 | 1–7 | 50 | 273.01 | 0.2 |
| | *Vibilia* spp. | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others | 1–8 | 21 | 0.99 | 0.3 | 1–3 | 33 | 19.18 | 0.2 |
| 10 | POLYCHAETA (3.20) | **4–40** | **16** | **0.40** | **0.5** | <1–7 | **83** | 118.21 | 1.7 |
| | Larvae | — | 0 | 0.00 | 0.0 | <1–4 | 33 | 103.81 | 1.5 |
| | Postlarvae | 4–40 | 16 | 0.40 | 0.5 | 3–7 | 50 | 14.40 | 0.2 |
| OTHER CATEGORIES | | | | | | | | | |
| Molluscan larvae | | — | 0 | 0.00 | 0.0 | <<1–<1 | 50 | 189.59 | 0.7 |
| Cladocera | | — | 0 | 0.00 | 0.0 | <1–1 | 33 | 142.20 | 0.8 |
| Cyclopoida | | NR | 1 | 0.01 | NR | <1–1 | 67 | 648.00 | 4.0 |
| Cirripedean larvae | | — | 0 | 0.00 | 0.0 | <<1–<1 | 67 | 128.70 | 0.2 |
| Reptantian larvae | | — | 0 | 0.00 | 0.0 | <1–6 | 83 | 52.20 | 0.3 |
| Natantian larvae | | — | 0 | 0.00 | 0.0 | 1–5 | 33 | 237.60 | NR |
| Bryozoan larvae | | — | 0 | 0.00 | 0.0 | <1 | 33 | 244.49 | 0.2 |
| Larvacea | | 2 | 3 | 0.12 | 0.1 | <1–4 | 67 | 844.20 | 2.8 |
| Chaetognatha | | 10–11 | 3 | 0.06 | 0.2 | 5–20 | 83 | 225.59 | 5.0 |
| Eggs, undetermined | | — | 0 | 0.00 | 0.0 | <1 | 17 | 1535.99 | 4.3 |
| Eggs, fish | | 3 | 1 | 0.01 | <0.1 | <1–2 | 33 | 40.19 | 4.4 |
| Fishes | | 6–24 | 4 | 0.04 | 0.2 | 4–20 | 33 | 5.40 | 0.7 |
| UNIDENTIFIABLE MATERIAL[5] | | — | — | — | 17.4 | — | — | — | — |

No. fish examined: 73
218–350, $\bar{x}$ = 290.3 mm SL
No. empty = 7
$\bar{x}$ no. prey: individuals = 32.4
taxa = 3.6

No. plankton collections: 6
$\bar{x}$ no. zooplankters: 9663.0

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[1] Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.

[2] *Velella velella* floats on the water's surface, where it was not effectively sampled by our net.

[3] NR = not recorded. The enumeration was either omitted or unfeasible.

[4] Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.

[5] Digested beyond recognition.

## DISCUSSION

It is clear that wind-driven movement of the surface water profoundly influences feeding by *Sebastes mystinus* off northern California. Water set in motion by the wind can be tens of meters deep (Bakun 1973; Barber and Smith 1981), and so carries most of the foods of nearshore planktivores. The movement is seaward (with upwelling) under northerly winds and shoreward (with downwelling) under southerly winds. Thus, with winds along the Mendocino coast being northerly or southerly about 80% of the time (based on records of the NOAA weather station there), adult *S. mystinus* in that area alternate between periods when planktonic foods are being carried into their habitat and periods when these foods are being carried away.

This perception of alternations between upwelling and downwelling is simplified, perhaps overly so, to emphasize features we consider essential to the feeding of *S. mystinus*, and also because details of what clearly is a complex oceanographic system remain unclear. In particular, we stress the importance of shoreward surface transport in carrying prey to *S. mystinus* in nearshore habitats. The major prey of adult *S. mystinus*—thaliaceans, pelagic hydrozoans, and other relatively large, gelatinous zooplankters—tend to be concentrated in areas of oceanic convergence, and dispersed in areas of oceanic divergence (e.g., Bakun and Parrish 1980). Thus, when offshore surface waters converge on the coast, the planktonic foods of *S. mystinus* become concentrated near shore.

TABLE 5.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of winter. $n = 4$.

| Food organism | | In diet | | | | In plankton | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 1 | THALIACEA (29034.03) | **7–20** | **71** | **12.90** | **31.7** | **5–45** | **50** | **9.90** | **34.8** |
| | Undetermined species | 7–20 | 71 | 12.90 | 31.7 | 5–45 | 50 | 9.90 | 34.8 |
| 2 | HYPERIIDEA (3278.81) | **1–5** | **62** | **23.40** | **2.2** | **1–6** | **75** | **2.25** | **0.8** |
| | *Hyperoche medusarum* | — | 0 | 0.00 | 0.0 | 4 | 25 | 0.45 | NR[3] |
| | *Vibilia* spp. | 1–5 | 57 | 23.06 | 2.1 | 5–6 | 25 | 0.90 | 0.8 |
| | Others | 6 | 5 | 0.34 | 0.1 | 1 | 25 | 0.90 | NR |
| 3 | EUPHAUSIACEA (1567.61) | **6–12** | **43** | **11.76** | **3.1** | **10** | **75** | **2.25** | **12.5** |
| | Larvae | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | *Thysanoessa* spp. | 6–12 | 38 | 11.67 | 3.1 | 10 | 75 | 2.25 | 12.5 |
| | Others | 6 | 5 | 0.09 | <0.1 | — | 0 | 0.00 | 0.0 |
| 4 | SCYPHOZOA (1054.20) | **NR** | **38** | **1.43** | **19.4** | **NR** | **NR** | **NR** | **NR** |
| | Fragments[2] | NR | 38 | 1.43 | 19.4 | NR | NR | NR | NR |
| 5 | PELAGIC GASTROPODA (726.34) | **6–30** | **48** | **2.91** | **5.2** | **1–20** | **25** | **8.10** | **0.8** |
| | Heteropoda | | | | | | | | |
| | *Caranaria japonica* | 15–30 | 10 | 0.24 | 0.5 | — | 0 | 0.00 | 0.0 |
| | Pteropoda | | | | | | | | |
| | *Corolla spectabilis* | 6–20 | 48 | 2.67 | 4.7 | 20 | 25 | 0.45 | 0.8 |
| | *Limacina helicina* | — | 0 | 0.00 | 0.0 | 1–2 | 25 | 7.65 | NR |
| | Others | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| 6 | PELAGIC HYDROZOA (437.91) | **3–13** | **43** | **1.52** | **6.7** | **1–6** | **75** | **14.85** | **1.3** |
| | Hydromedusae | | | | | | | | |
| | *Eutonina indicans* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others | 10–22 | 40 | 0.33 | 3.5 | 1–4 | 50 | 12.60 | 0.5 |
| | Syphonophora | | | | | | | | |
| | *Muggiaea atlantica* | 8–13 | 38 | 0.86 | 2.1 | 6 | 50 | 1.35 | 0.8 |
| | *Stephanomia bijuga* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
| | Others | 3–20 | 19 | 0.33 | 1.1 | 3 | 25 | 0.90 | NR |
| | Chondrophora | | | | | | | | |
| | *Velella velella* | — | 0 | 0.00 | 0.0 | NA[4] | NA | NA | NA |
| 7 | PLANTS (380.00) | **NR** | **38** | **NR** | **10.0** | **NR** | **NR** | **NR** | **NR** |
| | *Nereocystis* sori | NR | 5 | 0.10 | 0.1 | NR | NR | NR | NR |
| | *Porphyra* sp. | NR | 19 | NR | 5.2 | NR | NR | NR | NR |
| | *Smithora naidum* | — | 0 | 0.00 | 0.0 | NR | NR | NR | NR |
| | Others | NR | 19 | NR | 4.7 | NR | NR | NR | NR |

Shoreward transport can be either wind-driven (Ekman transport), or result simply from relaxation of the forces that drive upwelling. But in either case our observations indicate that shoreward flowing surface waters override the colder waters near shore, a process we refer to as downwelling. Usually the term downwelling is limited to conditions that result from shoreward Ekman transport (e.g., Gross 1977), but we have found that relaxation of upwelling has essentially the same effect on the nearshore ecosystem, the difference being simply in degree of effect.

Some studies have concluded that warming of the nearshore surface waters during relaxation of upwelling results from alongshore advection (e.g., Send et al. 1987), but even though zooplankters entering our study area during downwelling generally moved southward along the coast, the characteristic presence of such forms as thaliaceans, ctenophores, and pteropods indicate that the advection is from offshore. So despite the complexities of circulation and mixing that occur in the coastal waters off northern California (e.g., Winant et al. 1987), the net result affecting the trophic relations of *S. mystinus* are alternations between seaward and shoreward transport.

These water movements follow a strong seasonal pattern that is evident in upwelling indices for lat. 39°N (which crosses Mendocino) produced by the Pacific Fisheries Environmental Group of the Southwest Fisheries Center, NMFS, NOAA. In addition to the seasonal trend, short-term episodes of seaward and shoreward transport produce day-to-day, even hour-to-hour, changes in the foods available to

TABLE 5.—*Continued.*

| Food organism |  | In diet |  |  |  | In plankton |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Taxa (rank index) | Size (mm) | % occur. | $\bar{x}$ no. | $\bar{x}$ % vol. | Size (mm) | % occur. | $\bar{x}$ no.[1] | $\bar{x}$ % vol. |
| 8 | CTENOPHORA (4.73) | **11–20** | **10** | **0.43** | **1.1** | **—** | **0** | **0.00** | **0.0** |
|  | *Plerobrachia bachei* | 11 | 5 | 0.09 | 0.1 | — | 0 | 0.00 | 0.0 |
|  | Others | 20 | 5 | 0.34 | 1.0 | — | 0 | 0.00 | 0.0 |
| 9 | MYSIDACEA (4.47) | **6–20** | **14** | **0.29** | **1.2** | **3–8** | **50** | **1.80** | **0.5** |
|  | *Acanthomysis sculpta* | 6 | 5 | 0.19 | 1.0 | — | 0 | 0.00 | 0.0 |
|  | Others | 18–20 | 10 | 0.10 | 0.2 | 3–8 | 50 | 1.80 | 0.5 |
| 10 | CALANOIDA (1.18) | **2–5** | **14** | **0.28** | **0.3** | **1–5** | **100** | **684.00** | **25.6** |
|  | Nauplii | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
|  | *Acartia* spp. | — | 0 | 0.00 | 0.0 | <1–1 | 25 | 229.50 | 7.5 |
|  | *Calanus pacificus* | 2–3 | 14 | 0.14 | 0.1 | 1–3 | 100 | 110.70 | 3.8 |
|  | *Eucalanus californicus* | 5 | 10 | 0.14 | 0.2 | 3–5 | 50 | 12.60 | 0.8 |
|  | *Rhincalanus nasutus* | — | 0 | 0.00 | 0.0 | — | 0 | 0.00 | 0.0 |
|  | Others | — | 0 | 0.00 | 0.0 | 1–2 | 100 | 331.20 | 13.5 |
| OTHER CATEGORIES |  |  |  |  |  |  |  |  |  |
| Molluscan larvae |  | — | 0 | 0.00 | 0.0 | <<1–<1 | 50 | 38.70 | 2.5 |
| Cyclopoida |  | — | 0 | 0.00 | 0.0 | 1 | 75 | 61.20 | 1.5 |
| Cirripedean larvae |  | — | 0 | 0.00 | 0.0 | 1–2 | 75 | 24.75 | 0.5 |
| Reptantian larvae |  | 4 | <1 | 0.05 | <0.1 | <1–3 | 100 | 240.30 | 9.3 |
| Larvacea |  | — | 0 | 0.00 | 0.0 | 3–6 | 50 | 6.30 | 1.3 |
| Chaetognatha |  | — | 0 | 0.00 | 0.0 | 5–35 | 75 | 14.85 | 5.0 |
| Fishes |  | 8–10 | <1 | 0.10 | NR | 3–7 | 75 | 7.65 | 2.8 |
| UNIDENTIFIABLE MATERIAL[5] |  | — | — | — | 19.1 | — | — | — | — |

No. fish examined: 38
200–345, $\bar{x}$ = 265.3 mm SL
No. empty: 17
$\bar{x}$ no. prey: individuals = 45.2
taxa = 4.8

No. plankton collections: 4
$\bar{x}$ no. zooplankters: 634.3

[1] Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2] Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata*, which were avoided by us during plankton collections because they would have made collections unmanageable.
[3] NR = not recorded. The enumeration was either omitted or unfeasible.
[4] *Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5] Digested beyond recognition.

planktivorous fishes. The following discussion considers how the diet of *S. mystinus*, summarized in Figure 13, is influenced by these alternations in surface transport during distinct upwelling and downwelling seasons.

## The Upwelling Season

The spring-summer upwelling season produces optimal feeding conditions for *S. mystinus*. During this period the combined effects of increased nutrients (from strong upwelling) and increased daylight (from longer days, higher sun-angle, and less storm-produced sediments in suspension) result in growth of diatom populations that constitute the food-base of the zooplankton community.

Seaward Ekman transport in response to the season's persistent northerly winds carries the upwelled nutrients and increasing number of diatoms offshore, where the response of zooplankters can be spectacular. Consider, for example, thaliaceans, which are a major prey of adult *S. mystinus*. Recent study has shown that populations of *Salpa fusiformis* (a common thaliacean in the California Current) normally are food-limited, but can grow rapidly when diatoms are abundant (Silver 1975). In response to a diatom bloom, *Thalia democratica* (another salp common in the California Current), can increase in size by up to 10%/hour and in numbers up to 2.5 times/day, the highest rate recorded for a metazoan animal (Heron 1972a, b).

Zooplankters thus increased in size and number are then carried to *S. mystinus* near shore by the shoreward flow that develops with relaxation of upwelling, or, more forcefully, with shoreward Ekman transport under southerly winds. It remains uncertain, however, whether the numbers of zooplankters entering the Mendocino nearshore habitats are in fact related to the productivity of local upwelling. Wickett (1967) concluded that zooplankton abun-

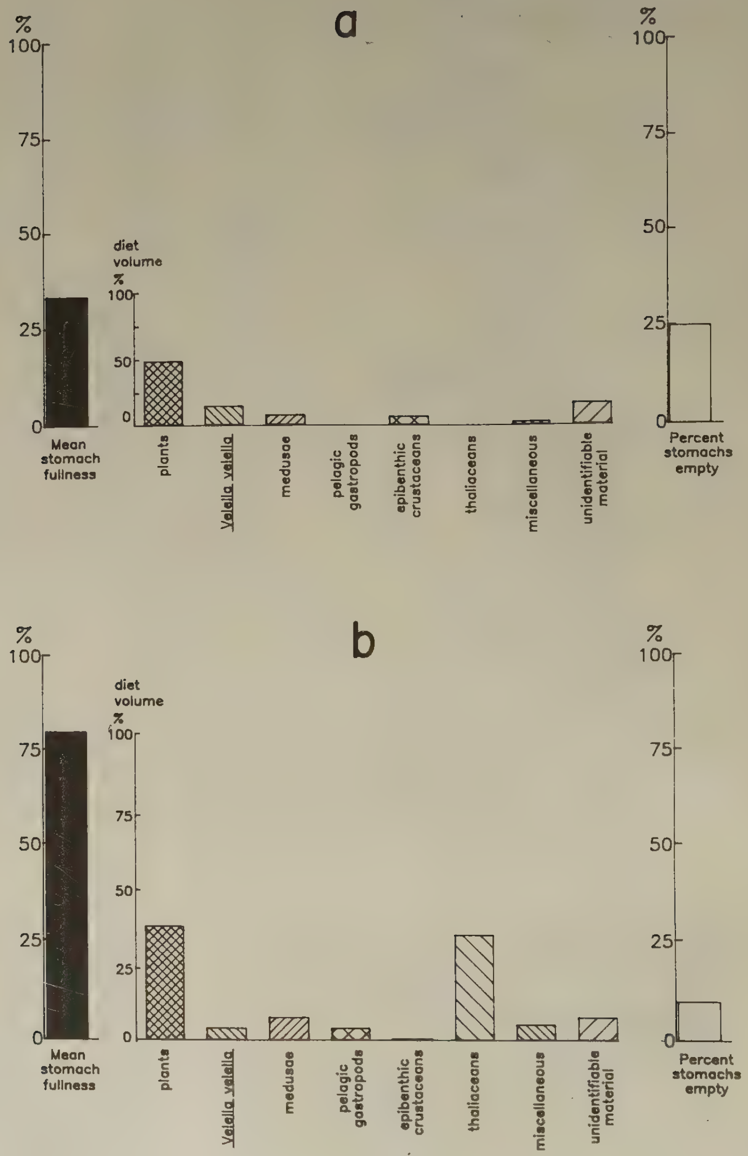

FIGURE 13.—Seasonal variations in the diet of *Sebastes mystinus*:

a. Diet during upwelling episodes of the upwelling season. $n = 51$.

b. Diet during downwelling episodes of the upwelling season. $n = 85$.

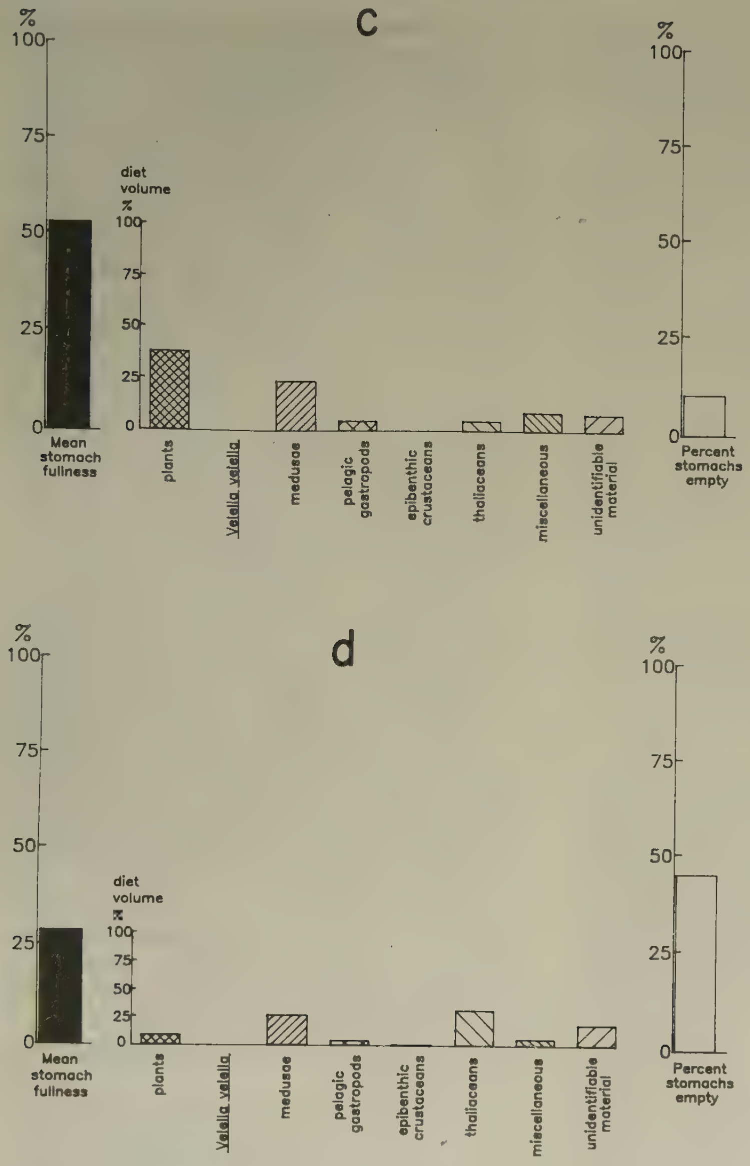

FIGURE 13.—*Continued*—Seasonal variations in the diet of *Sebastes mystinus*:

c. Diet during fall of the downwelling season. $n = 73$.

d. Diet during winter of the downwelling season. $n = 38$.

dances off California depend on nutrients from the Gulf of Alaska, and Chelton et al. (1982) concluded not only that phytoplankton off California depend on nutrients from higher latitudes but also that wind-forced coastal upwelling is relatively unimportant in supplying these nutrients. Despite this uncertainty, growth in thaliaceans is so rapid that it would seem at least many of those off the Mendocino coast could result from local upwelling. Regardless of what determines the growth of thaliaceans in this region, their appearance in large numbers next to the beach is evidence that shoreward transport has developed. These animals are readily detected by in situ observations, and also by their occurrences in samples of both plankton and gut contents (Table 3).

Intermittent shoreward transport during the upwelling season seems especially strong off northern California. This is evident in the upwelling indices of Bakun (1973), and also in that fewer thaliaceans get inshore at this time of year, both to the north, off Oregon (Hubbard and Pearcy 1971), and to the south, off central and southern California (Blackburn 1975). Thus, it is clear that the major foods of *S. mystinus* along the Mendocino coast are most available during downwelling episodes of the upwelling season.

Despite the increased productivity of the upwelling season, *S. mystinus* experiences relatively poor feeding conditions during that season's upwelling episodes. Not only are fewer prey taken during upwelling than during downwelling, a higher proportion of the fish have empty stomachs (Fig. 13). This is because the shoreward flow that transports zooplankters from offshore during downwelling is replaced by the seaward flow that is part of the upwelling condition.

There is, however, one relatively large gelatinous zooplankter from offshore that is most available as prey during upwelling. This is the chondrophore *Velella velella*, a pelagic hydrozoan known as "by-the-wind-sailor". It is, in fact, entirely because of this animal that the food category "Pelagic Hydrozoa" ranked second as food during upwelling episodes (Table 2). Because *V. velella* floats on the water's surface and is equipped with a sail-like structure (Fig. 8), its movements are determined more by wind than by current. The species includes two forms distinguished by whether their sails are oriented to the left of or to the right of the main body axis. This orientation determines their direction in sailing before the wind—left-handed individuals sail to the left of the wind direction and right-handed individuals sail to the right (Bieri 1959). Although it has been reported that the right-handed form predominates off California (Morris et al. 1980), all those we examined from off Mendocino were left-handed, and so would have been driven shoreward by the northerly winds that generated upwelling.

In the absence of favored open-water zooplankters, *S. mystinus* increased consumption of nearshore hyperbenthic zooplankton, e.g., mysidaceans and gammarideans (Table 2). But fewer of these organisms were taken than might be expected, based on their great abundance during much of the upwelling season. *Acanthomysis sculpta*, the mysid most often taken as prey, typically aggregates in large swarms within 2 m of the seafloor. To prey on them, adult *S. mystinus* must leave the upper levels of the water column in a departure from their usual feeding mode that may reduce feeding effectiveness. In addition, most hyperbenthic zooplankters probably are too small to be ready prey of these fish. Although 5–7 mm mysids (Table 2) should be large enough, most other taxa are less than 2 mm. Organisms as small as 1 mm occur in the diet, including some thought to be strictly benthonic, e.g., smaller of the gammaridean *Jassa* sp. (which also occurred in plankton collections; Table 2). But such forms may be ingested (and taken by plankton nets) while attached to drifting plant fragments. Although *S. mystinus* has a smaller mouth than most of its congeners, presumably as an adaptation to planktivory (Hallacher and Roberts 1985), the adults appear unable to consume the larvae of neritic species, e.g., cirripedeans, that, with maximum dimensions of 1 mm or less, often are the most numerous of the zooplankton (Table 2). These larvae are major prey of juvenile *S. mystinus* (unpubl. data; Gaines and Roughgarden 1987), which further suggests it is their small size that precludes them as prey of the adult.

Foods most often consumed in the absence of preferred zooplankters, however, were plant materials. In fact, during upwelling episodes more plants were consumed than anything else (Table 2), and even during downwelling plants were the second-ranked food category (Table 3). Although these rankings are inflated by undigested plant tissues, certain algal materials appear to be important foods. The availability of plant foods to supplement prey shortages was strongly seasonal, however. Thus, the sharply reduced availability of plants during winter and early spring undoubtedly contributed to the prevalence of empty stomachs among fish collected at those times.

Although a wide variety of plants were ingested, *S. mystinus* seemed able to utilize only certain algal tissues. These included zoospores of *Nereocystis leutkeana* and the two epiphytes, *Porphyra nereocystis* and *Smithora naidum*. Probably this is because as members of a carnivorous family they have only limited abilities to digest plant material.

The zoospores of *N. leutkeana* are especially vulnerable to *S. mystinus* when the sori have dropped from the plants' fronds, because at this time the sori have lost their epidermis (an adaptation of the mature sori that facilitates release of the zoospores (David C. Walker[2])). Zoospores may be appropriate food for this largely carnivorous fish because they are, as their name implies, animal-like: they have cell membranes but not the cellulosic cell walls (Wilson 1952) that preclude plants as food for many fishes (e.g., Lobel 1981). The other algae apparently utilized—*Porphyra nereocystis* and *Smithora naidum*—may be appropriate forage for a fish with limited herbivorous abilities because they are monostromatic plants only 25–60 μ thick (Abbott and Hollenberg 1976). So while Gotshall et al. (1965) reported that algae in the guts of *S. mystinus* generally are undigested, some forms appear to be important foods.

It is possible that plant materials are among items of little or no food value that are ingested during food shortages simply because at such times the adult *S. mystinus* become less discriminating in their choice of drifting objects. On the other hand, it is also possible that these fish have unusual herbivorous abilities as a result of adaptations to a diet rich in thaliaceans, which are among the few animals with cellulosic tissues (Berrill 1961). This second possibility is weakened, however, by the fact that the cellulosic tunics of the thaliaceans appear to pass through the gut undigested (Gotshall et al. 1965; our observations).

## The Downwelling Season

As the downwelling season developed in the fall, *S. mystinus* experienced progressively poorer feeding conditions. Offshore water flowing into the nearshore habitats at these times tended to be poor in phytoplankton (hence its transparency and blueness, in contrast to the turbid greenness of a few months before), and so generally lacked the herbivorous thaliaceans that were major prey during periods of peak feeding. Relatively large gelatinous zooplankters continued on occasion to be numerous in the shoreward flow, but the species at this time tended to be carnivores rather than herbivores, and *S. mystinus* did not feed on some of them. For example, while siphonophores made "Pelagic Hydrozoa" the top-ranked food category (Table 4), the most numerous pelagic hydrozoan in the water column, *Eutonina indicans*, went virtually untaken. (The small medusae visible throughout Figure 1, especially against the dark kelp, are of this species.) On the other hand, another relatively large, gelatinous zooplankter, the ctenophore *Pleurobrachia bachei* (Fig. 10), was prominent both as prey and in the plankton. Probably the presence of *P. bachei* accounted for the gut-content occurrences of the hyperiid *Hyperoche medusarum*, which is a parasite of this ctenophore (Brusca 1970).

As was true during late spring and summer, certain plant materials became major foods during the fall when favored zooplankters were in short supply. But unlike late spring and summer, when many different plant forms were taken, virtually the only plant materials consumed in the fall were the sori of *N. leutkeana*. This reflected a decreasing abundance of other plants in the environment at the time. Nevertheless, while sporophytes of *N. leutkeana* were fewer in fall than in summer, those present were larger, more mature, and produced more sori.

Although winter produced the poorest feeding conditions of the year, with by far the highest incidence of empty stomachs among the fish examined (Figure 13; also noted by Gotshall et al. 1965), occasionally the waters flowing into the nearshore habitats were rich in offshore zooplankters, including thaliaceans, and at these times the fish fed well. Our sampling of the highly varied winter conditions was not frequent enough to recognize a pattern, but they differed from fall conditions. In general, the distinctive fall and winter conditions off Mendocino matched the "oceanic" and "Davidson Current" oceanographic seasons defined by Skogsberg (1936) and Bolin and Abbott (1962) for Monterey Bay.

## Ekman Transport and the Distribution of *Sebastes mystinus*

Ekman transport may be important to the distribution of *S. mystinus*. This is implicit in our finding that alternations between seaward and shoreward surface transport produce feeding opportunities for which the species is particularly well adapted. Along the west coast of North America, these alternations are best developed off northern and central California (Bakun 1973; Bakun et al. 1974; Mason and Bakun 1985). And not only is *S. mystinus* most numerous off this same section of the coast, it is perhaps the dominant fish in the nearshore habitat there (Hallacher and Roberts 1985; Bodkin 1984; our observations). Although the species is reported from northern Baja California, Mexico, to the Bering Sea (Miller and Lea 1972), its numbers are sharply reduced northward from northern California (Alverson et al. 1964; Frey 1971; Hart 1973) and southward from central California (Hubbs 1948; Limbaugh 1955; Quast 1968). Although undoubtedly other factors are involved, we suggest that occurrences of *S. mystinus* in these northern and southern regions are limited by less favorable feeding conditions.

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[2] David C. Walker, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada, pers. commun. 10 May 1977.

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## LITERATURE CITED

ABBOTT, I. A., AND C. J. HOLLENBERG.
1976. Marine algae of California. Stanford Univ. Press, Stanford, 827 p.

ALVERSON, D. L., A. T. PRUTER, AND L. L. RONHOLT.
1964. A study of demersal fishes and fisheries of the northeastern Pacific Ocean. H. R. MacMillan Lectures in Fisheries. Inst. Fish. Univ. British Columbia, 190 p.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.
1975. Daily and weekly upwelling indices, west coast of North America, 1967-73. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.

BAKUN, A., D. R. MCLAIN, AND F. V. MAYO.
1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull., U.S., 72:843-844.

BAKUN, A., AND R. H. PARRISH.
1980. Environmental inputs to fishery population models for eastern boundary current regions. *In* G. A. Sharp (editor), Workshop on the effects of environmental variation on larval pelagic fishes, p. 67-104. Workshop Rep. 28, Intergov. Ocean. Comm., UNESCO. Paris.

BARBER, R. T., AND R. C. SMITH.
1981. Coastal upwelling systems. *In* A. R. Longhurst (editor), Analysis of marine ecosystems, p. 31-68. Acad. Press, N.Y.

BERRILL, N. J.
1961. Salpa. Sci. Am. 204:150-160.

BIERI, R.
1959. Dimorphism and size distribution in *Velella* and *Physalia*. Nature 184:1333.

BOJE, R., AND M. TOMCZAK (editors).
1978. Upwelling systems. Springer-Verlag, N.Y., 303 p.

BLACKBURN, M.
1975. Thaliacea of the California Current region: relations to temperature, chlorophyll, currents and upwelling. CALCOFI Rep. 20:183-214.

BODKIN, J. L.
1986. Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California. Fish. Bull., U.S. 84:799-808.

BOLIN, R. L., AND D. P. ABBOTT.
1962. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. CALCOFI Rep. 9:23-45.

CHELTON, D. B., P. A. BERNAL, AND J. A. MCGOWAN.
1982. Large scale interannual physical and biological interactions in the California Current. J. Mar. Res. 40:1095-1125.

EKMAN, V. W.
1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys. 2,11:1-52.

FREY, H. W. (editor).
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, 148 p.

GAINES, S. D., AND J. ROUGHGARDEN.
1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. Science 235:479-481.

GOTSHALL, D. W., J. G. SMITH, AND A. HOLBERT.
1965. Food of the blue rockfish *Sebastodes mystinus*. Calif. Dep. Fish Game 51:147-162.

GROSS, M. G.
1977. Oceanography. 2d ed. Prentice-Hall, N.J. 497 p.

HALLACHER, L. E., AND D. A. ROBERTS.
1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay. Environ. Biol. Fish. 12:91-110.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Ottawa, 740 p.

HERON, A. C.
1972a. Population ecology of a colonizing species: the pelagic tunicate *Thalia democratica*. I Individual growth and generation time. Oecologia (Berl.) 10:269-293.
1972b. Population ecology of a colonizing species: the pelagic tunicate *Thalia democratica*. II population growth rate. Oecologia (Berl.) 10:294-312.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S., 74:567-598.

HUBBARD, L. T., AND W. G. PEARCY.
1971. Geographic distribution and relative abundance of Salpidae off the Oregon Coast. J. Fish. Res. Board Can. 28:1831-1836.

HUBBS, C. L.
1948. Changes in the fish fauna of western North America

correlated with changes in ocean temperature. J. Mar. Res. 7:459–482.

LAVAL, P.
1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. *In* M. Barnes (editor), Oceanography and marine biology, annual review 18, p. 11–56. Aberdeen Univ. Press, Aberdeen.

LIMBAUGH, C.
1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif. Inst. Mar. Resour., IMR Ref. 55-9.

LOBEL, P. S.
1981. Trophic biology of herbivorous reeffishes: Alimentary pH and digestive capabilities. J. Fish Biol. 19:365–397.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habits of three switch feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257–271.

MASON, J. E., AND A. BAKUN.
1986. Upwelling index update, U.S. west coast, 33N-48N latitude. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-67, 81 p.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MORRIS, R. H., D. P. ABBOTT, AND E. C. HADERLIE.
1980. Intertidal invertebrates of California. Stanford Univ. Press, Stanford, 690 p.

PINKAS, C. M., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna and bonito in California Waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

REID, J. L., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies of the California Current system. CalCOFI Prog. Rep. 1/7/56 to 1/1/58, p. 27–90.

SEND, V., R. C. BEARDSLEY, AND C. D. WINANT.
1987. Relaxation from upwelling in the Coastal Ocean Dynamics Experiment. J. Geophys. Res. 92:1683–1698.

SILVER, M. C.
1975. The habits of *Salpa fusiformis* in the California Current as defined by indicator assemblages. Limnol. Oceanogr. 20:230–237.

SKOGSBERG, T.
1936. Hydrography of Monterey Bay, California. Thermal conditions, 1929–1933. Trans. Am. Phil. Soc. 29, 152 p.

SMITH, R. L.
1968. Upwelling. *In* H. Barnes (editor), Oceanography and marine biology, annual review, 6, p. 11–45. George Allen and Unwin Ltd., Lond.

QUAST, J. C.
1968. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109–142. Calif. Dep. Fish Game, Fish Bull. 139.

WICKETT, P.
1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. J. Fish. Res. Board Can. 24:581–594.

WILSON, C. L.
1952. Botany. Dryden Press, N.Y., 483 p.

WINANT, C. D., R. C. BEARDSLEY, AND R. E. DAVIS.
1987. Moored wind, temperature, and current observations made during Coastal Ocean Dynamics Experiments 1 and 2 over the northern California continental shelf and upper slope. J. Geophys. Res. 92:1569–1604.

8833

# Review of U.S. West Coast Commercial Shark Fisheries

DAVID B. HOLTS

*ABSTRACT—The economic history of elasmobranch fisheries generally indicates the need for a high catch per unit of effort because of fluctuating commercial value and market demand. Growth and reproduction in most elasmobranch species are extremely slow, and as a result there is a close relationship between stock size and recruitment. Because of this relationship, only a small amount of that stock is available to support a sustained fishery. The increased demand for shark as a food fish has put tremendous fishing pressure on some species. Two of these, the common thresher,* Alopias vulpinus, *and Pacific angel shark,* Squatina californica, *have not responded well to this increased pressure. Several other stocks appear healthy even though some warning signs of overfishing are appearing. The need for reduced fishing on some stocks and increased monitoring of catch for others is warranted.*

## Introduction

Commercial fishing operations directed toward various shark species have, in the past, been relatively short lived. A few shark fisheries, such as that for the spiny dogfish, *Squalus acanthias*, have been sustained over long periods. These fisheries generally produced minimum ex-vessel prices and fluctuating yields in a market with uncertain demand. Aggressive small-vessel fisheries grew on the U.S. west coast as new markets offering high yields and profits developed for shark meat. Responding to the new demand, these new fleets began landing large quantities of sharks. Elasmobranch fisheries such as the well-documented soupfin shark, *Galeorhinus zyopterus*, fisheries in the early 1940's and the recent decline of the drift gillnet (DGN) fishery for thresher shark, *Alopius vulpinus*, and the setnet fishery for Pacific angel shark, *Squatina californica*, in southern California are examples.

Although sharks are vulnerable to a wide variety of fishing gears, the primary reason they are not able to support high-yield fisheries is their apparent inability to respond to increased fishing pressure. Unlike teleosts, most elasmobranch species have a low rate of reproduction, slow growth, and relatively late maturity. Consequently, any rapid increase in fishing mortality can lower the rate of recruitment to a very low level. These facts are well documented (Ripley, 1946; Holden, 1973, 1974, 1977). When recruitment falls below the ability to respond to increased fishing pressure, that population will decline until fishing effort is reduced or the fishery collapses. Unfortunately, elasmobranchs are so vulnerable to overexploitation by expanding fisheries that long-term depletion problems may already exist before fishery managers are able to assess the problem with standard monitoring techniques and analysis. Notwithstanding the additional pressure from political and special interest groups, population declines for many of these stocks could continue for some time even if fishing effort were removed immediately.

## Background

Before the 1970's various species of shark were used commercially in the United States for food, vitamin-rich liver oils, pet food, leather, as curios, and for reduction to protein and fertilizer. These products did not generate much demand and only commanded mediocre market prices. Shark demand as a food fish began to increase on the west coast during the middle-1970's. Consumer response to this high protein, low fat meat was very good, and shark was finally accepted as a nutritious and flavorful alternative to red meat and the more traditional seafoods as well.

Ex-vessel prices for shark meat rose sharply in response to this consumer demand and several species of shark became important west coast fisheries. Thresher shark prices, for example, increased 500 percent between 1977 and 1986. West coast fish buyers paid increased prices for dressed Pacific angel, soupfin, and shortfin mako, *Isurus oxyrinchus*, shark (called bonito shark locally). They were also test marketing white shark, *Charcharodon carcharias*; salmon shark, *Lamna ditropis*; sevengill shark, *Notorynchus maculatus*; leopard shark, *Triakis semifasciata*; spiny dogfish, and other shark species as well. Markets that formally sold shark only as "grayfish," now advertised fresh shark at retail prices as high as $4 and $5 per pound. Commercial buyers were shipping fresh shark meat throughout the nation, and many prestigious restaurants featured shark meat in their specials and as the catch of the day. The growth in reported landings along the U.S. west coast over the past 12 years is shown in Table 1.

The tremendous success of these shark fisheries raised concerns that some stocks

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Table 1.—Commercial U.S. west coast and Mexican shark landings, 1974-86.

| Species | 1986[1] | 1985 | 1984 | 1983 | 1982 | 1981 | 1980 | 1979 | 1978 | 1977 | 1976 | 1975 | 1974 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pacific angel | 1,139,250 | 1,237,810 | 633,250 | 351,344 | 317,953 | 260,031 | 110,022 | 123,652 | 82,383 | 366 | 690 | 2,967 | 179 |
| Bigeye thresher | 46,184 | 119,632 | 74,769 | 106,507 | 36,269 | 10,542 | 10,842 | | | | | | |
| Blue | 2,850 | 2,356 | 3,940 | 13,983 | 57,838 | 202,898 | 192,130 | 83,966 | 35,904 | 98,365 | 9,928 | 497 | 46 |
| Bonito | 456,063 | 215,126 | 244,021 | 322,953 | 527,677 | 275,830 | 155,336 | 35,334 | 27,436 | 19,911 | 2,293 | 9,958 | 4,032 |
| Brown smoothhound | 13,506 | 33,312 | 8,091 | 14,101 | 5,263 | 23,641 | 5,783 | 2,440 | 7,365 | 264 | 20 | 20,000 | 150 |
| Common thresher | 1,215,165 | 1,528,766 | 1,662,587 | 1,757,353 | 2,386,585 | 1,937,618 | 1,806,002 | 735,602 | 302,073 | 129,522 | 46,887 | 37,729 | 2,225 |
| Cow | 439 | 427 | 1,333 | 1,258 | 1,328 | 771 | 438 | 290 | 249 | | 35 | | |
| Dusky | | | | 120 | | 196 | | | 103 | 202 | 50 | | |
| Gray smoothhound | 506 | 1,874 | 6,846 | 1,055 | 2,520 | | 761 | 12,046 | 33,745 | | | | |
| Horn | 197 | 363 | 613 | 485 | 7,541 | 2,286 | 8,465 | 21,055 | 273 | 1,156 | 60 | | |
| Leopard | 65,826 | 75,695 | 69,187 | 101,309 | 70,666 | 49,380 | 40,085 | 26,966 | 34,956 | 22,267 | 14,590 | 10,831 | 5,918 |
| Pelagic thresher | 237 | 640 | | 10,923 | | | | | | | | | |
| Salmon | 2,252 | 2,016 | | 230 | 996 | | | | | 77 | | | |
| Sevengill | 55 | 893 | 282 | 1,735 | 2,041 | 3,415 | 545 | | 84 | | | | |
| Sixgill | | 4 | 96 | 128 | | 317 | 12 | 20 | | | | | |
| Smooth hammerhead | 3,628 | 3,920 | 6,831 | 44,481 | 1,866 | 2,259 | | 304 | 1,025 | 1,860 | | | |
| Soupfin | 197,164 | 243,661 | 558,280 | 176,155 | 249,070 | 257,348 | 192,119 | 221,840 | 176,070 | 162,166 | 182,390 | 85,430 | 42,017 |
| Spiny dogfish | 9,061 | 2,837,927 | 7,649,393 | 5,398,532 | 4,591,551 | 4,831,846 | 7,141,280 | 9,445,000 | 6,522,003 | 5,813,147 | 22,697 | 179 | 868 |
| Swell | | 20 | 222 | | | | 163 | | 2,795 | | | | |
| Unspecified | 135,146 | 193,317 | 178,213 | 181,373 | 273,721 | 580,932 | 1,158,219 | 840,956 | 600,473 | 563,382 | 582,450 | 365,849 | 174,523 |
| White | 923 | 2,861 | 6,102 | 634 | 8,052 | 42 | 1,660 | 2,269 | | | | | |
| U.S. total | 3,449,340 | 6,500,620 | 11,107,244 | 8,481,489 | 8,541,837 | 8,439,352 | 10,823,862 | 11,551,740 | 7,826,837 | 6,812,685 | 862,090 | 533,440 | 229,958 |
| Mexico-Japan data | | | 72,767 | 729,878 | 421,169 | 319,118 | 41,896 | | | | | | |
| Grand total | 3,449,340 | 6,500,620 | 11,180,011 | 9,211,367 | 8,963,006 | 8,758,470 | 10,865,758 | 11,551,740 | 7,826,837 | 6,812,685 | 862,090 | 533,440 | 229,958 |

[1] Preliminary data.

probably could not sustain directed fishing pressure. This was particularly evident for the rapidly expanding effort directed at southern California thresher and angel shark fisheries. Complicating matters was the fact that little information necessary for management purposes was known about many of these species. Some basic life history information was known, or inferred, from related species, but few data on stock size, distribution and range, migratory behavior, age at maturity, fecundity, and mortality were available for most of the shark species undergoing increased exploitation. Additionally, the techniques for aging elasmobranchs were not worked out for most species, although some progress was being made (Cailliet et al., 1983).

In this paper, I review the current status of some of the more important shark fisheries along the west coast of the United States. Landings, fishing effort, and related biological and life history information are discussed for each species taken in these fisheries. Shark fisheries from Alaska and Canada (except British Columbia's spiny dogfish catch) have not been included in this review. General life history information included in the descriptions is summarized from Castro (1983) and Compagno (1984).

## Thresher Shark Fishery

The fishery for thresher sharks is centered off southern California, between San Diego and the Mendocino Escarpment, north and offshore of San Francisco. Three species, the common thresher, *Alopias vulpinus*, the bigeye thresher, *A. superciliosus*, and the pelagic thresher, *A. pelagicus*, are caught in the fishery, although the common thresher is the principal species.

All three forms are considered highly migratory throughout the warm and temperate areas of the oceans. They feed on squid and small schooling fishes, including clupeoids, scombroids, and several types of bottomfish. Fishermen have recently reported common threshers taking significant numbers of salmon off the coasts of Oregon and Washington, although this has not been described as a major prey species of the thresher. Although there are some differences in feeding behavior, all three forms are known to use their long tail to stun their prey before eating them. Neither the magnitude of the population nor the distribution of individual stocks is known. Stock structure is unknown and differences in size at maturity and number of offspring suggest that Pacific common threshers may be isolated from those in the Indian Ocean.

All three species are ovoviviparous. Females produce one litter each spring and mating occurs later that summer. Gestation lasts about 9 months. Litters usually consist of two, four, or six fully formed pups weighing 5-6 kg (12 pounds) each. Using x-radiography to delineate the circuli on 143 common threshers collected off California, Cailliet and Bedford (1983), prepared a von Bertalanffy growth curve. The growth curve indicated that females mature at about age 7 (390 cm total length), and males mature at about 5 years or about 333 cm. The sex ratio of common threshers from this population appears to be nearly equal, although sexually segregated schools do occur. Estimates of natural mortality are assumed to be low since pups are born fully formed and both the growth and reproduction rates are low.

Table 2.—Landings in the U.S. west coast thresher shark fishery, 1977-86.

| Year | California |  |  | Oregon |  | Washington |  | Total landings |  |
|---|---|---|---|---|---|---|---|---|---|
|  | No. of receipts | Weight |  |  |  |  |  |  |  |
|  |  | Common | Bigeye | Receipts | Weight | Receipts | Weight | Pounds | Metric tons |
| 1977 | 349 | 129,522 |  |  |  |  |  | 129,522 | 59 |
| 1978 | 433 | 302,054 |  |  |  |  |  | 302,054 | 137 |
| 1979 | 745 | 735,536 |  |  |  |  |  | 735,536 | 334 |
| 1980 | 880 | 1,806,002 | 10,842 |  |  |  |  | 1,816,844 | 824 |
| 1981 | 1,632 | 1,974,037 | 10,542 |  |  |  |  | 1,984,579 | 900 |
| 1982 | 1,851 | 2,386,585 | 36,269 |  |  |  |  | 2,422,854 | 1099 |
| 1983 | 2,804 | 1,707,256 | 68,010 | 1 | 1,155 | 4 | 24,471 | 1,800,892 | 817 |
| 1984 | 2,691 | 1,657,693 | 74,770 | 0 |  | 8 | 6,271 | 1,738,734 | 789 |
| 1985 | 2,153 | 1,528,766 | 119,632 | 0 |  | 0 |  | 1,648,398 | 748 |
| 1986[1] |  | 545,417 | 46,184 |  | 454,748 |  | 200,000 | 1,200,050 | 545 |

[1] Preliminary.

The fishery began as a minor operation with only about 15 vessels landing sharks primarily as a by-catch during more lucrative fishing operations. The growth of the fishery was also stimulated by the valuable take of swordfish, *Xiphias gladius*, and a favorable ruling by the California Fish and Game Commission (CFGC) to allow drift gillnet boats to land and sell swordfish. The ex-vessel price for common thresher increased from $0.29/pound in 1977 to $0.73/pound in 1980 and reached $1.60/pound in 1986. The fleet grew to over 200 vessels by 1980, and entry into the fishery became limited by law (Bedford and Hagerman, 1983). Swordfish was now the primary target of the California DGN fleet. By 1985 the number of licensed vessels totaled 227 with another 33 vessels holding permits to fish only north of Point Arguello, Calif.

During the spring, the common thresher is the primary target of this fishery in the northern area. The bigeye thresher is also commonly landed. Bigeye threshers have soft-textured meat that tends to shrink while cooking and has met with only moderate success in the fresh-fish markets. Landings have increased in recent years due to better handling methods. The pelagic thresher is rarely taken in the catch because of its soft and bitter tasting meat and low abundance in productive fishing areas.

Off southern California, highest catch rates occur in the spring. Fishing effort shifts to swordfish during the summer and fall months. Common threshers move into the Southern California Bight in the early spring for pupping and breeding. Large threshers appear to follow the warmwater isotherms northward into central and northern California areas, and good catches have been taken through August. Fishable stocks appear to be limited to within about 75 n.mi. of shore, islands, seamounts, or shallow banks. The southern extension of the population is unknown because U.S. commercial fishing boats are not permitted within the Mexican Fishery Conservation Zone. Mexican-Japanese joint ventures have operated long-line vessels off Baja California for many years. Although their primary targets are tunas and billfishes, substantial amounts of common and bigeye thresher sharks are reportedly landed. Catch statistics are not available for either species.

Prior to 1986, landings north of the Mendocino Escarpment were few. The 1982 and 1983 seasons were affected by a strong El Niño that caused warm waters to extend further north than normal. This warming condition may have caused a shift in the population centers of both the common and pelagic forms to the north. Oregon and Washington issued 3 experimental gillnet permits for thresher sharks in 1983 and 34 in 1984. Initial catches in 1983 indicated availability of fish outside southern California and possible expansion of the fishery. Most common threshers taken in 1983 were caught off central California, while bigeye and pelagic threshers were caught off southern California. Large catches in 1985 continued off central and southern California under normal conditions.

CFGC regulations implemented in 1986 were designed to reduce fishing mortality on the thresher shark populations. Already a limited entry fishery, these additional regulations included time and area closures, reduced the number of fishing days per season, and implemented new gear restrictions to 75 miles offshore. California vessels landed 380,390 pounds of common thresher and 38,079 pounds of bigeye thresher shark in this 30-day opening. At the end of this period, the fishery shifted to the north. Operating with experimental fishing permits these vessels produced good catches of common thresher off Oregon and Washington (Table 2). Under these permits (57 to Washington and 35 to Oregon) Oregon received 454,748 pounds from 33 vessels and 21 vessels landed 200,000 pounds in Washington's coastal ports. An additional 173,000 pounds were landed in California during the 1986 swordfish season.

The dressed weight of fish taken in these northern ports was in excess of 210 pounds, compared with the average of only 40 pounds for those taken off southern California. The sex ratio for these threshers was nearly even off California but catches off Oregon and Washington were mostly large males (Brian Culver, Wash. Dep. Fish. Personal commun., March 1986).

Although considered highly migratory, catch data indicate common threshers may have local population centers that move along the coast in relation to various environmental conditions. A tagging program to describe these movements is currently being conducted by the California Department of Fish and Game (CDFG), although results are not yet available. There is evidence in the literature (Compagno, 1984) of sexually segregated movements, and landing receipts of the current west coast fishery indicate threshers caught off Oregon and Washington were nearly all adult male. Such movements in other shark species tend to occur near the range limits of the population. This information along with the apparent shift of population centers during the 1982-1983 El Niño event suggests that this population, as a fishery stock, is not widely distributed but may be more geographically limited than previously thought.

Common thresher landings in California peaked in 1982 and they have declined since. Catch per unit of effort (CPUE) has decreased since the 1982 season (Bedford, 1985). Further evidence that the stocks are not able to support the current level of exploitation comes from the length-frequency data collected by the CDFG. These data show a steady decline in total length from 1981 to the present and that the number of subadult threshers has been significantly reduced off California. The catch off Oregon and Washington is dominated by large adults and has not included subadults to any extent.

From available evidence it is clear that the local thresher shark population is not large and that immigration from adjacent waters is not sufficient to sustain the current fishing pressure. This was first speculated by Hanan (1984). The fishery has been in a steady decline since 1983 and the CDFG has decided that "the California drift gill net shark fishery may be in precarious condition" (Bedford, 1985); the causes of that condition are discussed by Bedford (1987).

## Pacific Angel Shark Fishery

The fishery for the Pacific angel shark, *Squatina californica*, started in 1978 as an offshoot of the very successful Pacific halibut, *Hippoglossus stenolepis*, setnet fishery near Santa Barbara, Calif. This fishery is currently undergoing tremendous growth similar to that of the local thresher shark fishery. This small- to medium-sized, bottom dwelling shark is reported to occur in shallow coastal waters from Alaska to Baja California. It is the only species of the family Squatinidae in the north Pacific and is reported to be extremely abundant around Santa Barbara and the California Channel Islands.

The angel shark is a nocturnal fish, foraging at night for bottom and epibenthic fishes and squid. It is relatively inactive during the day, resting on the bottom sand or mud with only its eyes and back exposed. Angel sharks tagged with ultrasonic transmitters at Santa Catalina Island (Isthmus Cove) exhibited maximum activity periods at dusk and at midnight (Standora and Nelson, 1978). Tagging also showed that angel sharks have a home range and will return to the same general area after a night of foraging. More recent tag return data further support the home range concept, but also indicate that some angel sharks circumnavigate the local islands and can move across the Santa Barbara Channel from the mainland to the Channel Islands (John Richards, Sea Grant Marine Adviser, Goleta, Calif. Personal commun., Feb. 1986). Seasonal changes in the population centers have not been shown in the local areas, although Standora and Nelson (1978) suggest that angel sharks are more plentiful in June and July than in the winter months.

The life history and distribution of the angel shark may be the least known of any of the sharks supporting a major west coast fishery. Reproduction is ovoviviparous, but has not been described in the literature for this species. Both male and female angel sharks mature at about 90 to 100 cm. Females have a gestation period of 10 months and bear an average of six fully formed young per litter, each averaging 255 mm long (Natanson 1984). Parturition occurs from March through June, followed by mating. Determination of growth rates and age has so far been impossible with standard methods. Angel sharks are born with 6-7 growth bands in their vertebrae, and apparently one or more growth bands are laid per year in a manner not fully understood. Natanson (1984) believes the rate of band deposition is related to somatic growth rather than annual, seasonal, or lunar cycles. The whole process may be complicated by major physiological events and possibly prolonged gestation (Cailliet et al., 1983).

The fishery began expanding after initial development and marketing problems were worked out in 1976. The major portion of this fishery occurs in and around Santa Barbara and the Channel Islands. The greatest catch is taken in waters <20 m deep and within 1 mile from shore (Collins et al., 1984; Collins et al., 1985). The angel shark fishery has not spread north of Point Conception and only incidental landings have occurred in Oregon and Washington. Prior to 1982 only 6-8 California vessels fished for angel sharks. Fishing effort increased in 1982 as the El Niño caused the northern displacement of other preferred species. California landings jumped to 317,000 pounds in 1982, doubled by 1984, and reached 1.3 million pounds in 1985. Ex-vessel prices paid to fishermen rose from $0.15/pound in 1978 to $0.45 in 1984. Landings of 1.1 million pounds in 1986 marked the first decline in catch since the fishery began expanding.

The CPUE estimates are only preliminary at this time but do not appear to be decreasing. The length-frequency of observed catch has just begun to show signs of decreasing. The future of this fishery is very much in question. There are no published growth rates or longevity estimates for this species. Little is known of the angel shark's distribution north or south of the Channel Islands where fishing pressure is greatest. There is no information to suggest that fishable quantities of angel sharks exist very far to the north or south of the Channel Islands or that immigration from surrounding areas is occurring. The few facts that are known suggest angel sharks are vulnerable to directed fisheries.

Currently there are no regulations for the angel shark fishery other than general state and county regulations for all set net use. The CDFG has proposed new regulations that will limit the size and style of nets used, times and areas fished, and size limits for small fish. This fishery warrants close scrutiny and possible precautionary action to forestall what some fishery biologists see as an almost unavoidable overexploitation of the local angel shark population.

## Shortfin Mako or Bonito Shark Fishery

The shortfin mako, *Isurus oxyrinchus*, is known locally as the bonito shark. It is taken as a welcome by-catch by California drift gillnet vessels. Like several members of the family Lamnidae, the bonito shark is found in all tropical and temperate oceans and in both coastal and open ocean habitats. They are highly migratory and are considered one of the fastest and most active predators. Both adults and juveniles are abundant off California and Baja California in the summer months.

Reproduction is ovoviviparous with 2-10 pups per litter. Gestation is about 1 year, with parturition occurring in late spring. Pratt and Casey (1983) used silver nitrate to delineate the circuli in the vertebra to construct a von Bertalanffy growth curve for 109 Atlantic-caught shortfin mako sharks. They determined that the age of maturity was 2 years for males and 6 years for females. The growth rate of males and females was similar although females grew larger. There are no mortality estimates (natural or fishing) for this species. The size in the catch is small (the average is 9-14 kg, dressed), but the length-frequency profile has not declined. Few landings have been reported north of California (only 10 percent in 1983 and none in 1984).

The bonito shark has good quality meat and is the object of long-line fisheries throughout the world. The California catch is almost entirely composed of juveniles taken in the drift gill net fishery for thresher sharks and swordfish. These small bonito sharks bring a wholesale price of $0.75-$1.25/pound.

Many southern California anglers consider the bonito shark a prime game fish because the fish fights and jumps when hooked. Shark derbies have become increasingly popular in recent years and if the trend continues, these catches may contribute significantly to overall landings.

Catch rates, length frequency, and estimates of CPUE provide little information on the magnitude, structure or distribution of the bonito shark stock(s). Estimates of CPUE are not reliable because the bonito shark is an incidental rather than a target species. Catch rates increased dramatically in 1980, peaked in 1982, and declined over the following three seasons. Although this decline in catch may indicate the first signs of overfishing, it may also have been caused by a change in fishing strategy aimed at thresher sharks or even a result of a population shift brought on by the 1982 El Niño. Landings were back to normal in 1986, length-frequency data have not changed, and there is no evidence that this stock has been significantly altered by current fishing pressure.

This fishery should continue to be monitored until there are sufficient data to assess the strength of the stock(s). Declines could occur if increased fishing effort were directed at the bonito shark, especially adults, or if stocks are smaller than expected.

## Soupfin Shark Fishery

The soupfin shark, *Galeorhinus galeus*, has a long history of involvement in commercial fisheries. In addition to the west coast fishery, the soupfin (also called the school shark and tope shark) is fished in the southwest Atlantic, off South Africa, and off the southern coast of Australia. This species supported the large and well publicized fishery off California (and South Africa) in the late 1930's and early 1940's. Those fisheries focused on the vitamin-rich liver oil of the soupfin but collapsed due to overfishing and the advent of synthetic vitamin A developed during World War II.

In the eastern Pacific Ocean the soupfin shark is found in the temperate continental and insular waters north and south of the equator. It is an active, coastal-pelagic shark found from the surf line, shallow bays, and submarine canyons to depths near 500 m in some offshore areas. It is highly migratory and travels in small schools. This species exhibits marked sexual segregation, with adult males favoring the northern range, although in central California there are equal proportions of males and females. Major pupping areas are south of Point Conception. The current fishery is centered off southern California, with moderate production in Oregon and Washington.

Reproduction is ovoviviparous with one litter of 6-52 pups per year. Mating occurs in the spring with gestation lasting 12 months. Pups average about 35 cm at birth. Size at maturity for females is about 130-185 cm with maximum size to 195 cm. Males mature at 120-170 cm and reach a maximum of 175 cm. Females mature at about 11 years and males mature at 8 years of age. Growth of the California soupfin was described by Ripley (1946) from data collected during the early fishery.

The flesh of the soupfin provides an excellent market product. A small west coast fishery persisted until the late 1970's when other shark meat became popular. Both the commercial and sport fishery for soupfin shark is currently expanding off our west coast, with annual production in excess of 100 metric tons.

There is little current information concerning the structure of the west coast soupfin population. Holden (1977) estimated the unexploited, north Pacific stock at 29,000 tons. It is unlikely that population levels have returned to these pre-War levels, although there are no current mortality estimates. The southern distribution of the fishery stock extends well into Mexico, but catch records are not available from the Mexican fisheries.

The California fishery is centered off San Diego and Orange Counties. Commercial soupfin operations occur throughout the year, but landings are greatest between September and December. Soupfin sharks are usually caught at <180 m and within 5 miles of shore. In California there are no fishing regulations directed at the soupfin shark other than those imposed on all set nets. Soupfin sharks are also taken in small numbers by related fisheries such as those for halibut, sea bass and angel shark. Current landings for California indicate increased fishing pressure in response to the overall increased demand for shark meat. In Oregon, vessels landed 9,100 pounds in 1985. Most of this occurred in the winter months and most (62 percent) was landed in Astoria. The fishery is managed by the Pacific Marine Fishery Council (PMFC). There are no data at this time to indicate current fishing pressure has affected the local soupfin shark populations.

## Blue Shark Fishery

The blue shark, *Prionace glauca*, is not a current target species of any west coast fishery. However, it is taken in large numbers by the California drift gill-net fishery for thresher shark and swordfish. The blue shark is common throughout all tropical and temperate waters both offshore and inshore. It may be the most common pelagic shark in the world and is common off both U.S. coasts. Blue sharks are highly migratory and individuals tagged off the U.S. east coast have made trans-Atlantic crossings (Casey, et al., 1982). Blue sharks are also known to make extensive, sexually segregated migrations, although local collections indicate large individuals of either sex are uncommon off California. Juveniles abound in southern California coastal waters in the spring and summer months. In the spring, individuals tagged in the waters off Catalina Island exhibit a movement pattern toward the island at dusk and return to the deeper waters in the predawn hours. This pattern is not seen in the summer and fall months (Sciarrotta and Nelson, 1977).

The blue shark is one of the most prolific of pelagic sharks and has a viviparous mode of reproduction. Gestation lasts 9-12 months and litter size varies between 25 and 50 pups (up to 135 have been reported). A von Bertalanffy growth curve based on silver nitrate aging techniques for 130 blue sharks indicates females mature at 5-6 years of age (220 cm) and males at 4-5 years (Cailliet and Bedford, 1983). There are no estimates of mortality.

Preliminary estimates indicate that about 15,000-20,000 (300 metric tons) blue sharks are taken incidentally in other fisheries each year. Gillnet caught blue sharks are unmarketable because the urea in the muscle tissue rapidly breaks down into ammonia soon after death and tainting the meat. A small, one-vessel, experimental longline fishery developed off southern California from 1980 to 1982. This vessel resolved most of the processing problems and produced a good quality product. The warm water conditions of 1982 and 1983 displaced the blue shark population out of the Southern California Bight and interrupted this trial fishery. The blue sharks returned to southern California in the fall of 1983, although the participants in the experimental fishery have not renewed their efforts.

The impact of the drift gillnet operations on the blue shark population has been severe at times, although currently there is no west coast fishery directing effort at the blue shark. Determining incidental fishing mortality from both drift and setnet fisheries is very difficult because the incidental catch of blue shark is dumped at sea. Current catch estimates are lower than in the past because fishermen are using larger mesh nets that catch fewer small sharks and because they tend to avoid areas with a high concentration of blue sharks. These facts along with the fish's relatively high fecundity suggest that the continuing incidental catch has not resulted in a reduction in the local blue shark population.

## Spiny Dogfish Fishery

The spiny dogfish, *Squalus acanthias*, is one of the most abundant sharks in cool temperate waters throughout the world's oceans. This small bottom dweller is a very important commercial species and is fished wherever it occurs. In the northeast Pacific the spiny dogfish is common in both inshore and offshore areas of the continental and insular shelf and is commercially abundant off British Columbia and Washington.

The spiny dogfish is a slow and moderately inactive swimmer. At times, large, sexually segregated schools are formed. They are opportunistic feeders on small bottom and epibenthic fish and some pelagic fish such as herring. The composition of prey species varies considerably depending on location, time, and depth. Occasionally large, mixed feeding aggregations of both sexes and all sizes will form. These schools have caused severe losses to fishermen as a result of damaged fishing gear and lost fishing time and catch. The preferred water temperature is 7°-15°C and these sharks will make vertical depth migrations to remain in their comfort zone. Tagging studies conducted in British Columbia and Washington indicate that spiny dogfish are indigenous to the inland waters of Puget Sound, Strait of Georgia, and Hecate Sound, and that there is considerable movement across the U.S.-Canadian border in both directions. These results also showed that less than 2 percent of those tagged in these inland waters were recovered in the open sea. Although some individuals have made extensive movements, both to the south and to the west (2,320 and 7,890 km, respectively), the fishable stocks appear to move only with the seasonal changes in water temperature (Ketchen, 1986).

Reproduction in the spiny dogfish is extremely slow because of the 2-year breeding cycle of the females. They are ovoviviparous and breeding occurs in the fall and early winter months. Litter size is from 1 to 20, but averages only 6-8 fully formed pups after a gestation period of 18-24 months. Growth is exceptionally slow with maturity averaging 14 years for males and 24 years for females. Females mature between 70 and 100 cm and live at least 30-50 years, with some estimates approaching 100 years. Males mature at 59-72 cm and reach a maximum size of 83-100 cm.

The fishery for Pacific dogfish has gone through several stages of growth and decline since before World War II. Traditional use has been for various food products, for export to European and Oriental markets, for reduction, and as fertilizer in the domestic market. Use of the spiny dogfish for food in the U.S. began about 1975. Primary use was for fresh, smoked, and processed meat. Continued growth of this fishery was encouraged by a strong European import market that was suffering from decreased production in the northeast Atlantic. Combined catches of spiny dogfish exceeded 2,600 metric tons in 1976, peaked at 4,681 metric tons in 1979, and has declined in recent years to about 2,600 metric tons (Table 3). U.S. fishing boats operated in Puget Sound where 99 percent of the west coast production was taken, with only incidental landings reported for Oregon and California.

The British Columbia catch followed the same pattern of expansion. Canadian vessels operate primarily in the south coast areas, which accounts for over 90 percent of their catch. Substantial amounts are also taken in Hecate Strait, although production in more distant and coastal fishing areas is limited by the lack of processing plants and the need for immediate processing of the catch. Total catch from these areas also peaked in 1979 with 4,757 metric tons landed

(Table 3), but then declined to an average of 3,000 metric tons between 1982 and 1985.

Although these catch figures seem to indicate a stable fishery, there are some warning signs of overfishing. Several important fishing areas such as Puget Sound and the southern parts of the Strait of Georgia show a decrease in abundance. Depending on the type of fishery, estimates of CPUE give a mixed look at abundance. Canada's setline fishery shows no increased effort in the Strait of Georgia between 1979 and 1982. On the other hand, CPUE for the trawl fishery in the same area fell steadily from 0.631 to 0.160 metric tons/haul between 1977 and 1982 (Ketchen, 1986). At this time there is no clear indication of the continued stability of this fishery. The economics of this fishery require a high catch per unit of effort because of the low commercial value, the need for close proximity to a processing plant, and a fluctuating market demand.

Estimates of stock size in the northeast Pacific varied between 300,000 and 500,000 metric tons before the great liver fishery during the 1940's. Over 250,000 metric tons of spiny dogfish were caught during this period. Current estimates of maximum sustained yield (MSY) range in the neighborhood of 8,000 to 10,000 metric tons.

Management of the spiny dogfish fishery is under the PMFC groundfish plan.

**Table 3.—Annual catch of spiny dogfish in the northeastern Pacific in metric tons, round weight[1].**

| Year | British Columbia | Wash. | Oregon | Calif. | Total |
|---|---|---|---|---|---|
| 1970 | 137 | 61 | 8 | | 206 |
| 1971 | 128 | 12 | 2 | | 142 |
| 1972 | 116 | 20 | tr | | 136 |
| 1973 | 5,056 | 6 | tr | | 5,062 |
| 1974 | 1,070 | 749 | 11 | tr | 1,830 |
| 1975 | 713 | 508 | 10 | tr | 1,231 |
| 1976 | 242 | 2,635 | 6 | 10 | 2,893 |
| 1977 | 1,730 | 2,462 | 122 | 174 | 4,488 |
| 1978 | 3,126 | 2,759 | 59 | 200 | 6,144 |
| 1979 | 4,757 | 4,284 | 344 | 53 | 9,438 |
| 1980 | 4,544 | 3,232 | 135 | 7 | 7,918 |
| 1981 | 1,782 | 2,185 | | 7 | 3,974 |
| 1982 | 3,914 | 2,032 | | 3 | 5,949 |
| 1983 | 3,051 | 2,423 | | 25 | 5,499 |
| 1984 | 2,441 | 3,461 | | 8 | 5,910 |
| 1985 | 2,680 | 1,287 | tr | tr | 3,967 |

[1] Sources: California Department of Fish and Game, Marine Statistics (1970-84); Washington Department of Fisheries, Statistical Reports (1976-84); Ketchen, 1986.

The MSY and available biological catch (ABC) for Washington have been proposed at 2,900 metric tons (Pedersen and DiDonato, 1982) and the MSY for British Columbia was set at 8,000-10,000 metric tons (Ketchen, 1986). The west coast stock appears healthy, even though there are some warning signs of overexploitation. There is an urgent need for a management policy between the United States and Canada to ensure a stable fishery for the spiny dogfish in the inland areas.

## Shark Fisheries in Mexico

Shark fishing in Mexico is poorly documented. Artisanal fisheries and cooperative fishing camps catch various species of sharks, skates, and rays for subsistence uses, as fresh fish for local markets, and as curios. There are also up to two Mexican longline vessels that target exclusively for thresher and mako sharks. Records are essentially nonexistent for most of these catches. The greatest amount of sharks taken off Baja California is by long-line joint venture operations with Japan.

Japanese long-line vessels have been fishing off the coast of Baja California since the early 1960's. The principal targets of these operations are striped marlin, *Tetrapturus audax*; sailfish, *Istiophorus platypterus*; swordfish, and tunas. Sharks are taken incidentally and delivered to markets in Mexico; the more expensive fish are delivered to Japan.

As many as 18 vessels operated from these ports between 1980 and 1984. These cooperative fishing operations were temporarily suspended between 1984 and early 1986. Currently, Japan and Korea each have six longline vessels licensed to operate out of Ensenada, B.C., Mex. There are an additional three active longliners operating from Mazatlan, and one from Manzanillo.

Catches of all shark species are combined into one shipboard reporting category, and the catch of individual species is not recoverable. Although the species composition is unknown, both common and bigeye threshers and bonito sharks reportedly make up the major portion of the shark catch. These records indicate combined shark catches represent up to 33 percent by weight (42 percent by number) of the total longline catch (Table 4). The reported shark catch for these vessels averaged 234 metric tons between 1981 and 1983.

**Table 4.—Landings and CPUE of Mexican-Japanese joint venture fisheries operating in Baja California. The number and weight of sharks listed here should be considered a minimum due to reporting irregularities.**

| Year | No. of sharks | Metric tons | Year | No. of sharks | Metric tons |
|---|---|---|---|---|---|
| 1980[1] | 290 | 19 | 1983 | 17,377 | 331 |
| 1981 | | 181 | 1984[1] | 1,394 | 33 |
| 1982 | 8,949 | 191 | | | |

[1] Incomplete data.

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## Literature Cited

Bedford, D. W. 1985. Pelagic shark/swordfish drift gillnet fishery. Calif. Dep. Fish Game, DFG Manage. Inf. Doc., 75 p.

__________. 1987. Shark Management: A case history—The California pelagic shark and swordfish fishery. *In* S. Cook (editor), Sharks: an inquiry into biology, behavior, fisheries, and use. p. 161-171. Oreg. State Univ. Ext. Serv., Corvallis.

__________ and F. B. Hagerman. 1983. The billfish fishery resource of the California current. CalCOFI Rep. XXIV:70-78.

Cailliet, G. M., and D. W. Bedford. 1983. The biology of three pelagic sharks from California waters, and their emerging fisheries: A review. CalCOFI Rep. XXIV.

__________, L. K. Martin, D. Kusher, P. Wolf, and B. A. Welden. 1983. Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:157-177.

Casey, J., H. W. Pratt, and C. Stillwell. 1982. The shark tagger. 1982 Summary. Newsletter of the Cooperative Shark Tagging Program. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Cent., 8 p.

Castro, J. I. 1983. The sharks of North American waters. Tex. A&M Univ. Press, College Sta., 180 p.

Collins, R. A., M. M. Vojkovich, A. R. Hartman, and R. J. Reed. 1984. Southern California nearshore gill and trammel net study 1983. Calif. Dep. Fish Game, Progress Rep., 33 p.

__________, __________, and R. J. Reed. 1985. Progress Report. Southern California nearshore gill and trammel net study 1984. State of California, DFG, July, 1985. 40 p.

Compagno, L. J. V. 1984. Sharks of the world. FAO Species Catalogue. Fish. Synop. 125, Vol. 4, Pt. 1, 2.

Hanan, D. A. 1984. Analysis of the common thresher shark (*Alopias vulpinus*) in the California Bight. U.S. Dep. Commer., NOAA, Natl. Mar. Fish Serv., SWFC Admin. Rep. LJ-84-10C, 34 p.

Holden, M. J. 1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164:360-367.

________. 1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* F. R. Jones (editor), Sea fisheries research, p. 117-137. J. Wiley & Sons, N.Y.

________. 1977. Elasmobranchs. *In* J. A. Gulland (editor), Fish population dynamics, p. 187-215. J. Wiley & Sons. N.Y.

Ketchen, K. S. 1986. The spiny dogfish (*Squalus acanthias*) in the northeast Pacific and a history of its utilization. Can. Spec. Publ. Fish. Aquat. Sci. 88, 78 p.

Natanson, L. J. 1984. Aspects of the age, growth and reproduction of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. Master's Thesis, Dep. Biol. San Jose State Univ., 71 p.

Pederson, M., and G. DiDonato. 1982. Groundfish management plan for Washington's inside waters. Wash. Dep. Fish. Prog. Rep. 170, 123 p.

Pratt, H. L., Jr., and J. G. Casey. 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*. *In* E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Fishes: Tunas, Billfishes, and Sharks, U.S. Dep. Commer., p. 175-177. NOAA Tech. Rep. NMFS 8.

Ripley, W. E. 1946. The biology of the soupfin, *Galeorhinus zyopterus*. Calif. Dep. Fish Game, Fish Bull. 64:7-37.

Sciarrotta, T. C., and D. R. Nelson. 1977. Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. Fish. Bull., U.S. 75(3):519-528.

Standora, E. A., and D. R. Nelson. 1978. A telemetric study of the behavior of free-swimming Pacific angel sharks, *Squatina californica*. S. Calif. Acad. Sci.

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## Comments on the role of objectives in fisheries management.

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The paper by Marasco and Miller contains four basic messages. First, fishery management objectives are multifaceted, include political and economic factors, and are not "scientific" *per se*. Decisions, and therefore management objectives, are political. Science can inform decision-makers but does not establish the objectives. The second message is that Councils do not establish polished and unambiguous objectives at the outset of a planning process, but rather objectives emerge as outcomes of the plan development process. Written objectives at the initial stage of Fishery Management Plan development tend to be, like those in the Magnuson Fishery Conservation and Management Act (MFCMA), grandly stated, but vague and inconsistent. The authors provide a realistic description of Regional Fishery Management Council decision-making, noting that management problems are "ill-structured", that Council members operate under conditions of limited rationality, and that many of the management decisions involve shifting benefits among competing groups.

Third, drawing upon the theory of organizational decision-making, Marasco and Miller argue that the classical view of technical decision-making, which makes a clear statement of objectives the first order of business, is not applicable to the decision environment of Fishery Management Councils. The authors contend that fishery councils cannot, and should not be expected to enunciate clear objectives to guide evaluation and selection of alternative management approaches. Finally, they submit four propositions for applied fisheries science which, they claim, would assist applied fishery science to play a major role in helping fishery managers to "muddle through". They recommend that scientists (a) use a multidisciplinary (holistic) approach, (b) assign proper disciplinary expertise to research topics, (c) avoid interdisciplinary bickering, and (d) stick to the role of finding and interpreting facts rather than assuming the role of policy maker. On the whole this paper presents a useful critique of the notion that fishery management is technical decision-making. It also realistically describes the context and content of the policy making process within the Regional Fishery Management Council system.

In my view, however, Marasco and Miller miss out on the broader role of standard fishery management objectives in setting the research agenda, and they prescribe too narrow a role for scientific/technical experts in the management process. I contend that the biological and economic objectives discussed in the literature of fisheries provide important constraints to management options, and that the special values widely held by fisheries professionals play a unique role in the management process. Acting as both expert advisor and advocate for professional values creates an ethical/professional dilemma for scientists in public policy debate. The remainder of my comments will focus on two issues: (1) the role of objectives in defining and clarifying the role of technical experts, and (2) the role of objectives in delimiting the scope of delegated action or investigation.

Each profession involved in fisheries management is predisposed to accept certain basic values, and these values represent unwritten objectives that have a profound influence on the menu of options and evaluations presented to decision makers. The interests and ethical commitments common to fishery biologists and resource economists appear explicitly in the MFCMA, and they frequently surface in the wording of proposed management objectives. Preservation of individual species and maintenance of "healthy" (i.e. abundant) fish populations are ethical commitments prevalent in fisheries biology. Some biologists see conservation of fish stocks not as a means to satisfy man's desires, but as an end in itself. The extreme depth of this commitment is reflected in the view that the fish population itself is the primary client of the fishery manager (Wright, 1981; p 38).

Similarly, pursuit of economic efficiency and an equitable distribution of income (or at least an equitable distribution of opportunities) are commonly held commitments in the economics profession. Economists are not satisfied with maintaining "healthy" fish populations, but seek also to minimize the costs of taking the allowable yield. They are frequently impatient with regulations that bestow unjustified monetary gains on special interest groups. Economists often see themselves as defenders of the general interest as against the special interests. These widespread professional viewpoints motivate and inspire much research, and guide the formulation of technical advice.

I view these professional predispositions as a necessary and constructive element of the system. Professional values lend a sense of purpose and ethical self-confidence to experts having no personal stake in management. Without them the technical work would likely deteriorate under the continual political pressure of self-interested resource users.

Marasco and Miller recognize that scientists, lacking clear instructions from the Council, may unduly insert their own value judgments into the planning process. That is, professional values may be translated into specific management objectives without adequate political input. But it is unreasonable to ask that intelligent and concerned advisors, acting with minimal guidance, develop management options and analyses that ignore their own viewpoints. By ignoring the other horn of this dilemma, the paper misconstrues the role of technical advisors.

The conflicting roles of experts need to be openly discussed. The scientists do act, and, I would argue, are expected to act, as partisans for more conservative harvest policies. Economists are expected to advocate efficiency, and sociologists/anthropologists are expected to look out for the interests of small (especially rural or minority) communities. Experts are part of the process, and they cannot be cast in the role of detached specialists. Fishery scientists need to recognize their multiple roles and to distinguish clearly between technical information and advice based upon personal values and circumstances.

A unique aspect of most technical advice is that it is slanted not by self-interest, but by a special kind of altruistic interest. This gives the expert's information more credence than that of self-interested spokesmen, and it lends consistency and transparency to expert recommendations. In my view, fishery managers are less likely to be misled by biologists counseling conservative quotas or economists seeking efficient harvest policies, than by advisors with no known professional position. Ideally the experienced fishery managers would recognize the various roles and ethical commitments represented by all their advisors. This frees the technical experts to shift between technical information and advice-giving roles with a minimum of confusion.

Marasco and Miller are correct to worry that the technical experts (as well as other advisors) may take over too much of the decision makers role. But this worry is inconsistent with the authors' claim that Councils should not be pressed to provide objectives at the outset of the management process. What is to be substituted as guidance to planning teams and advisory groups? The scientists are there to inform the politics, but it is unclear how information requirements are to be established if not through something like a set of objectives. If scientists are not to take policy into their own hands, how are they to begin the task of management planning, and what is the Council's responsibility in setting the agenda?

Since Council members must delegate most of the work in developing management regulations to teams of experts, initial objectives in the planning process must play a crucial role in controlling delegated authority and guiding subsequent policy evaluation. The objectives provide guidance as technical experts sort through a huge number of options to pick a comprehensible few for consideration directly by the Council. Through the process of plan development, therefore, some specific objectives should be established before significant amounts of planning are completed.

These comments deal with the broader and more complex question of how to use expert advice to make wise decisions in a representative democracy. There is no simple solution. Currently, the economics profession is undergoing a self-conscious re-examination of its role in public policy. As Nelson (1987, p.50) recently noted, "Economists coming into direct contact with government decision making have found that they cannot limit their role to that of neutral technicians; to do so would be to make themselves irrelevant and ultimately excluded." The role of advocate is not taught to economists, and much of the expert work done by economists does not call for advocacy of economics principles. Yet the effectiveness of economics thinking in forming public policy depends upon advocacy skills exercised by "insiders" (e.g. experts retained by decision makers) much more than it depends upon the virtuosity of academic research projects. Fishery biologists clearly face a similar need to advocate effectively for their conservation ethic.

In summary, although the paper by Marasco and Miller makes important distinctions between science and politics, I feel that it is unrealistic in calling for technical advisors to avoid advocating professional values, and that it is incorrect to view all objectives as outcomes of the policy process. Marasco and Miller are correct that allocations of fishery benefits and choices among competing objectives must be resolved by policy decisions, and that the outcomes imply original objectives. However, neither professional values and ethics nor the objectives established by the Council to limit the range of technical evaluation are "outcomes of the policy process". Prior objectives do and should have an important role to play in the formation of policy options and in controlling the scope of technical analysis.

## REFERENCES

NELSON, R.H. 1987. The economics profession and the making of public policy. Journal of Economic Literature 25, 49-91.

WRIGHT, S. 1981. Contemporary Pacific salmon fisheries management. North American Journal of Fisheries Management 1, 29-40.

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# Managing Alaska Groundfish: Current Problems and Management Alternatives

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# I. Introduction

Groundfish stocks in the Gulf of Alaska (GOA) and the Bering Sea and Aleutian Islands (BSAI) present U.S. fishery managers with a dilemma: they offer huge potential economic rewards, and they present unusually complex management problems. Recent U.S. fishery policy has promoted domestic fishery development as a means of capturing benefits from the potential $2 billion (processed value) groundfish industry in the 200-mile Exclusive Economic Zone (EEZ) off Alaska. This "Americanization" policy assigns highest priority to U.S. fishing in quota allocations, and it creates incentives for foreign nations to assist in developing the U.S. fishery. Given the recent expansion of the U.S. groundfish industry, the policy can be considered a substantial success. However, a large U.S. trawl fishery may damage traditional fisheries for other high-valued fish and shellfish stocks off Alaska. Also, continued rapid growth in fishing capacity threatens to create the usual problems of overcapitalization: much reduced profitability, short and disorderly fishing seasons, and intense pressure on conservation agencies to slacken fishing regulations. These problem areas create difficult challenges for the fishery management system.

Traditional domestic fisheries off Alaska specialize on high-priced fish, such as salmon, roe herring, pink shrimp, halibut, sablefish, and king and tanner crab. As recently as 1980, low-priced groundfish (e.g., pollock, Pacific cod, flounders, and rockfishes) accounted for less than 1% of the landed fish value in Alaska. During the past decade, a large number of small, coastal vessels, of the traditional owner-operator type, have routinely landed small quantities of high quality groundfish in various fishing ports of Southeast Alaska and around the Gulf of Alaska. Alaska Department of Fish and Game statistics for 1985, for example, indicate that close to 700 vessels using longline, hand troll, and power troll gear landed about 8,400 metric tons (exvessel value of $8 million) of sablefish, rockfish, pacific cod, and other saltwater finfish.

Before 1976, U.S. groundfish management actions were limited to controlling incidental catches of salmon, king crab, and halibut by foreign fisherman. Several bilateral agreements with Japan and the Soviet Union negotiated in the 1960s and early 1970s included prohibitions on foreign trawling in areas and seasons of unacceptable incidental catches or of direct conflicts with U.S. fishermen.[1] To obtain foreign cooperation, the U.S. allowed foreign fleets to fish, or to engage in provisioning or loading operations in the U.S. contiguous zone (12-mile zone).

With the enactment of the Fishery Conservation and Management Act of 1976, later changed to Magnuson Fishery Conservation and Management Act (MFCMA), U.S. sovereignty in the EEZ permitted more comprehensive regulation of foreign and domestic fishing. Fishery management plans developed by the North Pacific Fishery Management Council (NPFMC) have established a framework for setting annual harvest quotas, allocating quotas among foreign and domestic fishermen, allocating harvests among areas and gear types, reserving and later releasing harvest quotas, and adjusting in-season quotas and allocations. The management plans also regulate trawl catches of prohibited species (halibut, tanner crab, king crab, salmon) by setting limits on such catches and by closing certain areas to trawl fishing.

The MFCMA permits foreign fishing in the U.S. zone to the extent that the fish would not be harvested by domestic fishing, and requires that catch available to foreign fishing be allocated among nations based upon such criteria as adherence to fishing regulations, contributions to scientific research on fish stocks in the EEZ, and the extent to which the foreign nations foster the growth of U.S. fishery. Starting in 1978, and more strongly after amendment to the MFCMA in 1980, the Department of State tied foreign fishing privileges in the EEZ to market access and trade policy. Nations that impose tariff or non-tariff barriers to importation of U.S. fish products were given low priority in allocations of allowable foreign catch. Moreover, the so-called "Fish and Chips" policy, provided larger allocations to foreign nations that assisted in developing the U.S. industry through joint ventures, transfer of technology, or agreements to purchase U.S. processed fishery products (National Marine Fisheries Service (NMFS), 1985).

In addition to the national, pro-development fishery policy, the availability of many capable fishing vessels and an advantageous world market situation for frozen cod blocks and fillets spurred the development of the groundfish fishery. Scores of vessels originally built as combination crabber/trawlers for the king and tanner crab fishery off Alaska were suddenly looking for alternative fisheries when the crab fishery "crashed" in the early 1980s. In the BSAI, for example, the crab fishery peaked with 377 vessels landing 237 million pounds (all species) worth $144 million exvessel in 1980. The total harvest dropped to 134 million pounds ($98 million) in 1981 and 67 million pounds ($93 million) in 1982. As the crab fishery continued to decline over the following three years, many vessel owners became eager to experiment with alternate fisheries, including groundfish off the west coast and Alaska.

World prices for high-volume groundfish products, such as frozen fillets and blocks, rose steadily but unspectacularly through the 1970s and early 1980s. According to NMFS Operation Price Watch data (reported in an unpublished paper by Lewis Queirollo and Joseph Terry) the nominal retail price for the U.S. cod market rose from about $1.08/lb in 1973 to $2.37/lb in 1985. After correcting for inflation using the Consumer Price Index, this represented a slight drop in real domestic price for cod. Prices for other frozen groundfish products followed suit. During 1986, however, a sharp decline in Atlantic cod production caused a supply shortfall and an abrupt rise in frozen cod prices. The price per pound for a standard layer/shatter-pack of 3-5 oz. Alaska pollock fillets rose from $.85 in early 1986 to $1.50 in early 1987. This price rise was clearly attenuating by the end of 1987, but the overall effect on profits and investment prospects in the groundfish industry was highly encouraging.

A third factor was the decline in the international exchange rate for the dollar. During 1985 through 1987, the Japanese yen/U.S. dollar exchange rate fell from 255 to 146 yen/$. Even with steady internal Japanese prices for surimi, fillets and headed-gutted groundfish, U.S. groundfish operators able to deal in the Japanese market could experience significantly increased profits opportunities.

The several economic inducements noted above spurred growth in the U.S. fishery in two distinct stages. The first stage involves joint ventures with U.S. fishing vessels delivering to foreign at-sea fish processors. Many of the U.S. trawl vessels acting as catchers came from the king crab fleet. By 1986, around 125 U.S. joint venture vessels caught 1.4 million metric tons of groundfish, and the U.S. catch exceeded the foreign catch in the EEZ off Alaska for the first time. The joint venture fishing fleet is now capable of taking the full sustainable yield of most groundfish stocks that can be efficiently caught by trawl gear.

The second stage, expansion of groundfish processing capacity, is proceeding rapidly but is currently far behind domestic fishing capacity. The Arctic Trawler, outfitted to produce frozen cod fillets, initiated the U.S. factory trawl fleet in 1980.[2] Once the profitability of domestic at-sea groundfish processing was proven, more and more firms launched new or converted factory trawlers. The reported 1986 harvest by U.S. factory trawlers exceeded 80,000 metric tons. In 1987, at least twenty-five domestic factory trawlers and motherships, ranging in size from about 120 to 335 feet in length, are currently operating or in final stages of preparation for operating in Alaskan waters. In addition, thirty or so coastal trawl vessels are delivering to new groundfish processing facilities in coastal ports, such as Kodiak, Sand Point, Akutan, and Dutch Harbor, Alaska. It is likely that both shore-based plants and at-sea processors will continue expanding while the joint venture catches will decline somewhat.

As noted earlier, the domestic fishery expanded in response to high groundfish product prices and to priority treatment for U.S. fishing in quota allocations. Record high groundfish prices were caused mainly by shortages of north Atlantic cod during the last few years. As the shortages are alleviated prices will decline. In fact, prices for frozen cod and pollock fell about 20 percent in late 1987. The pace of future growth in the groundfish industry will depend upon continued high worldwide demand for frozen groundfish products, access to Asian markets for frozen headed and gutted fish, access to the Japanese market for surimi, and a growing U.S. consumer demand for frozen fillets, blocks, and surimi-based products.

The surprisingly rapid growth in U.S. fishing and processing capacity has spawned some concern that continuation of the current management regime will encourage too much investment in fishing capacity. Overcapitalization of the fishing fleet may ultimately trigger a well-known list of fishery ills: shortened fishing seasons, increased discard of prohibited species, and reduced economic returns from the fishery. Further, with continued free access to other Alaska fisheries, excess fishing capacity leaving the groundfish fishery could crowd into the crab, herring, and halibut fisheries.

An additional problem is a potentially serious degradation in fishery information. Foreign and joint venture catches are routinely monitored at sea by U.S. observers aboard processing ships. The foreign observer program is funded by fees charged foreign fishing nations. A comparable program for domestic processing vessels, catcher vessels, and catcher/processors is not in effect, and it seems highly unlikely that a domestic observer program approaching the 95% coverage obtained in the foreign fishery will be implemented soon. Without systematic at-sea sampling to determine species and size composition of trawl catches, to check prohibited species incidental catch rates and to monitor compliance with other regulations, the effectiveness of the harvest quota system may become suspect.

In response to various emerging management problems, the NPFMC recently announced its intention to develop and adopt a limited access system for the sablefish longline fishery, to consider adopting a possible cut-off date for further entry to the groundfish fishery, and to initiate a study of alternative limited access systems for groundfish. The Council has also established special committees to investigate and make recommendations regarding prohibited species catch regulations and domestic observer programs. The urgency of developing comprehensive and effective management approaches to all aspects of groundfish management increases as U.S. investment in the fishery proceeds at a rapid pace.

The purpose of this study is to review the current problems in the fishery, to sort through the various regulatory options, and to analyze the advantages of various feasible approaches. Any evaluation of modified regulations must be based upon an accurate perception of the current fishery status, management regime, and policy objectives. To fill this need, the following section of this report provides a synopsis of the state of the groundfish fishery and of the current management regulations. Section III delineates some criteria for evaluating a new management system. The subsequent sections discuss the use of conventional fishery regulations, and the elements of limited access systems. The final section of the report sums up the findings and makes various recommendation on the design of future groundfish management measures.

## Endnotes to Section I

1. See R.A. Fredin (1987) for an extensive history of groundfish regulation in Alaskan waters.
2. Trans-Pacific Seafoods' Arctic Trawler was originally built under a Federal fishery development program. The 296-foot freezer trawler and a sister ship (originally named the Sea Freeze Atlantic and Sea Freeze Pacific) were built at great expense and launched with much ballyhoo in 1968. This experiment was ahead of its time, as both ships proved unprofitable, and it failed to usher in the promised era of large-scale American groundfish trawling. Ironically, both sister ships have now been re-converted by private owners to fulfill their original tasks. The Arctic Trawler is undergoing still another conversion and will emerge as a surimi trawler.

# II. An Overview of the Fishery

## Size of the Fishery

Groundfish stocks in the Gulf of Alaska, Bering Sea, and Aleutian Islands (Figures 1 and 2) are among the largest and most valuable food fish resources in U.S. waters. During the past twenty years, annual groundfish harvests from Bering sea and Aleutian Island stocks ranged from 1 million to slightly over 2 million metric tons, while harvests from the Gulf of Alaska stocks have ranged from 78 thousand to 357 thousand metric tons (Figures 3 and 4). During 1984 through 1986 total harvests averaged 1.9 million metric tons per year in all areas combined. To place this in perspective, groundfish harvests from the U.S. zone represent about 27 percent of the total harvested throughout the north Pacific and Bering Sea (including FAO Zones 67 and 61), and are about 3 percent of the world food fish harvest (FAO, 1987).

As a percentage of total harvest, walleye pollock is the predominant species in both the BSAI and GOA (Figures 5 and 6). The next largest annual harvests in BSAI are for yellowfin sole, Pacific cod, other flatfish, and Atka mackerel. Following pollock in the GOA are Pacific cod and sablefish. Based upon recent unprocessed fish prices (ex-vessel and joint venture prices) the value of Alaska groundfish averaged about $256 million during 1984 to 1986. The value of processed products depends upon species and product category (e.g fresh fillets, headed and gutted fish, fillets in "shatter-packs," frozen blocks, roe, and surimi), product yields (i.e., pounds of product made per pound of raw fish), and product prices. Based upon prices, product yields, and distributions of fish to product categories reported in various publications and in interviews with groundfish industry participants, the total estimated product value from 1984 to 1986 was almost $1.4 billion per year.[1]

If the 1988 Acceptable Biological Catch (ABC) of each species were caught and sold at equivalent prices, the unprocessed market value would grow to $617 million (Table 1), and the potential processed product value (Table 2) could be over $2 billion. This total product value would be achieved only if: (a) all stocks abundances and market prices hold up to current levels, and (b) the domestic fishery is geared up to produce these harvest levels. Due to low stock abundances, or low market demands, or restrictive groundfish regulations (e.g., restrictive quotas or by-catch limits) annual harvests of some groundfish species have not been near the estimated long-term sustainable yields.

Stocks not being harvested near estimated MSY levels include Pacific cod (both BSAI and GOA stocks), and various flatfish species in GOA. Pacific cod catches in the Bering Sea averaged twice the estimated MSY during 1984-86 on the strength of two very large year classes spawned in 1977 and 1978. In the Gulf of Alaska, Pacific cod have been harvested well below sustainable yields. The NPFMC has designated a level of Optimum Yield (OY) that is only half the estimated

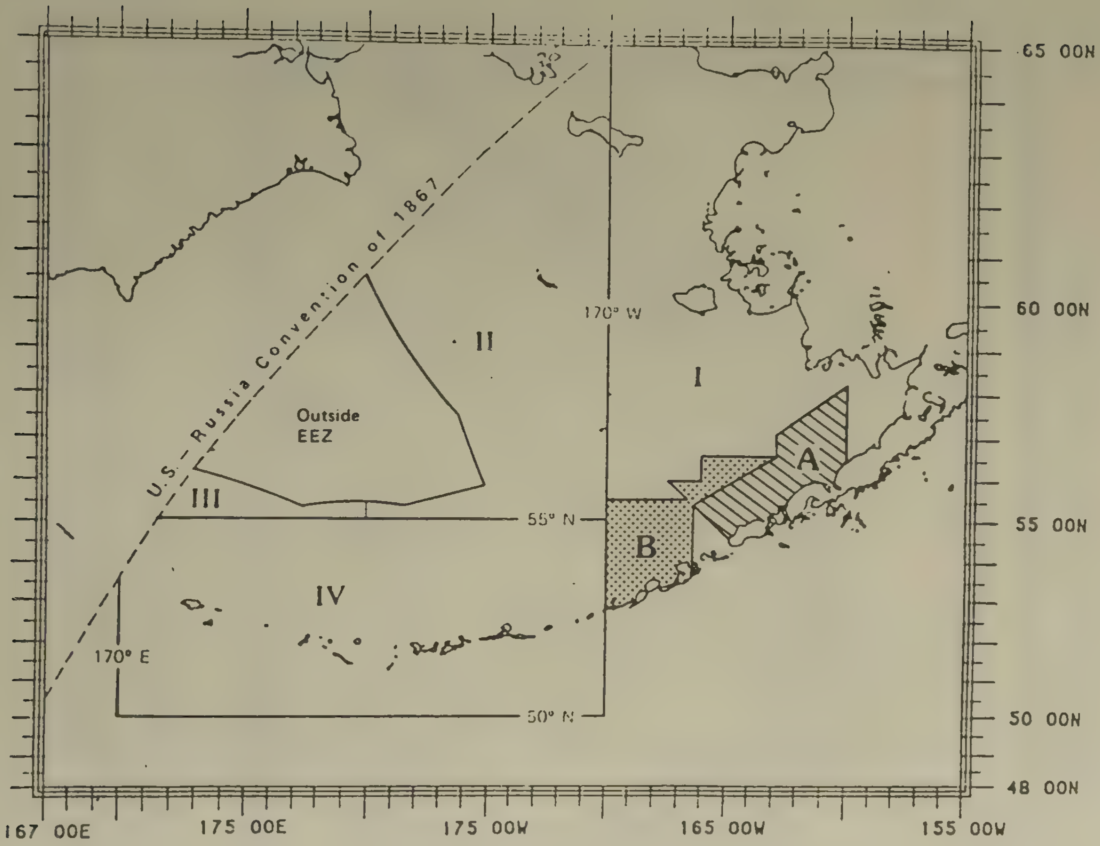

65 00N
60 00N
55 00N
50 00N
48 00N
167 00E
175 00E
175 00W
165 00W
155 00W
U.S. - Russia Convention of 1867
Outside EEZ
I
II
III
IV
A
B
170° W
55° N
50° N
170° E

Figure 1. Statistical zones and special fishing areas in the Bering Sea and Aleutian Islands.

MSY, ostensibly to protect sablefish; and the Total Allowable Level of Foreign Fishing (TALFF) has been drastically reduced by arbitrarily allocating most of the quotas to domestic fishing. Pacific ocean perch stocks have been chronically overfished since the 1960s, when distant water fishing fleets from the Soviet block fished them very hard. Flatfish stocks in GOA are lightly fished due to lack of market demand for some species (e.g., Arrowtooth flounder), and because the harvest quotas for these species have been kept intentionally low to reduce the bycatch mortality of Pacific halibut.

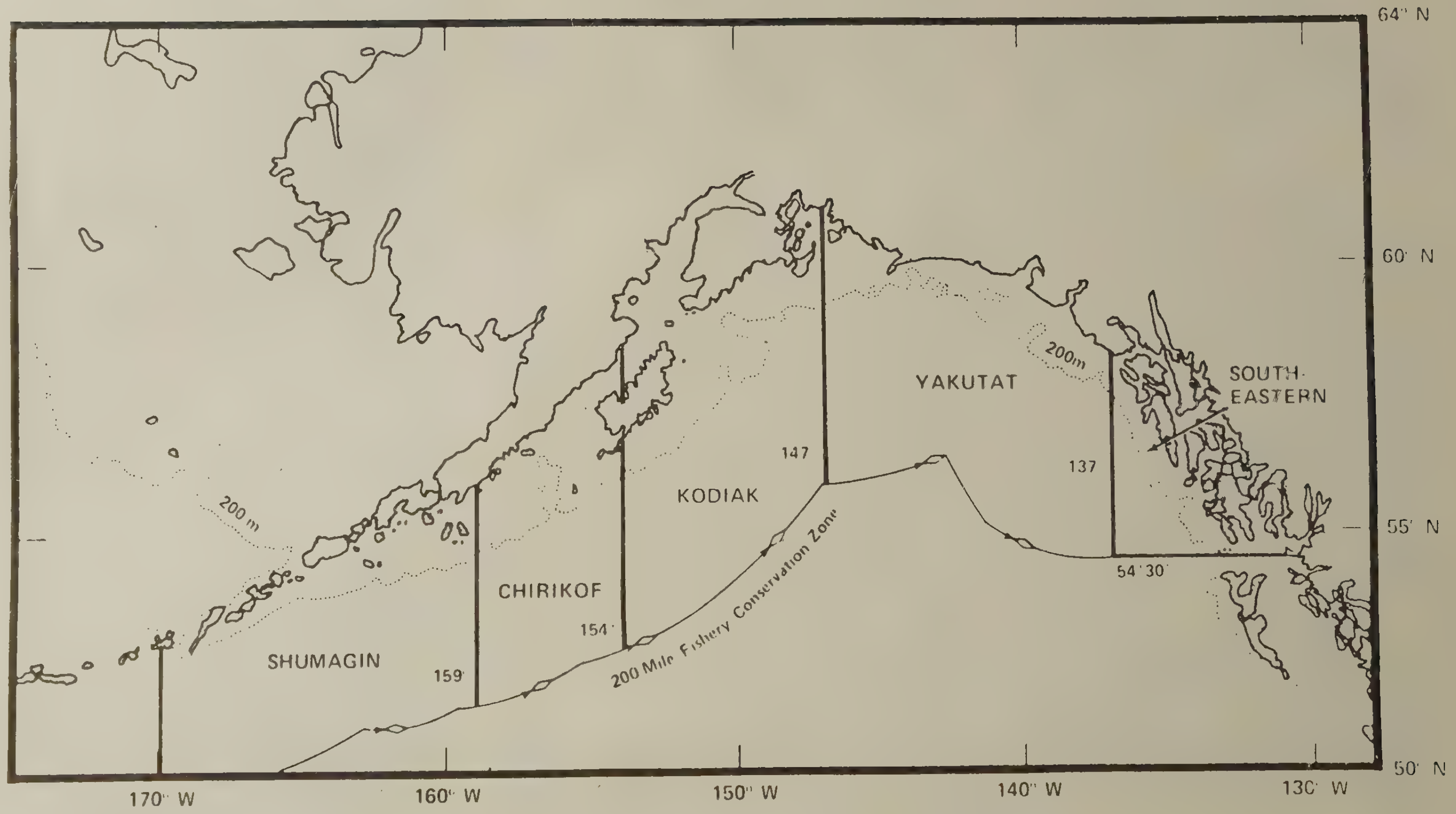

64° N
60° N
55° N
50° N
170° W
160° W
150° W
140° W
130° W
SHUMAGIN
CHIRIKOF
KODIAK
YAKUTAT
SOUTH-
EASTERN
159°
154°
147
137
54°30'
200 m
200m
200 Mile Fishery Conservation Zone

Figure 2. Statistical areas in the Exclusive Economic Zone in the Gulf of Alaska.

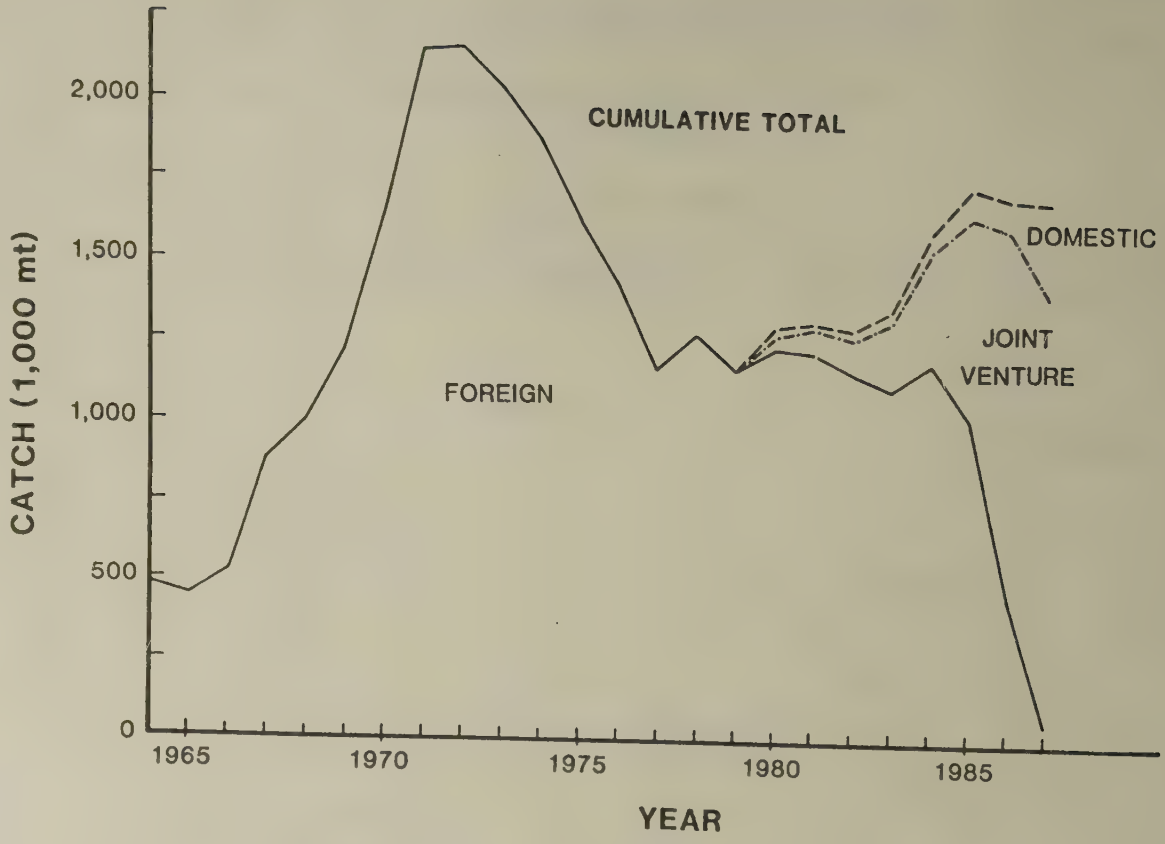


Figure 3. Annual groundfish harvests in the Bering Sea and Aleutian Islands.

Sources: Bakkala, R. G. and J. W. Balsiger, eds. (1987); Berger, J. D., J. E. Smoker and K. A. King (1986); and Smoker, J. E., personal communication.

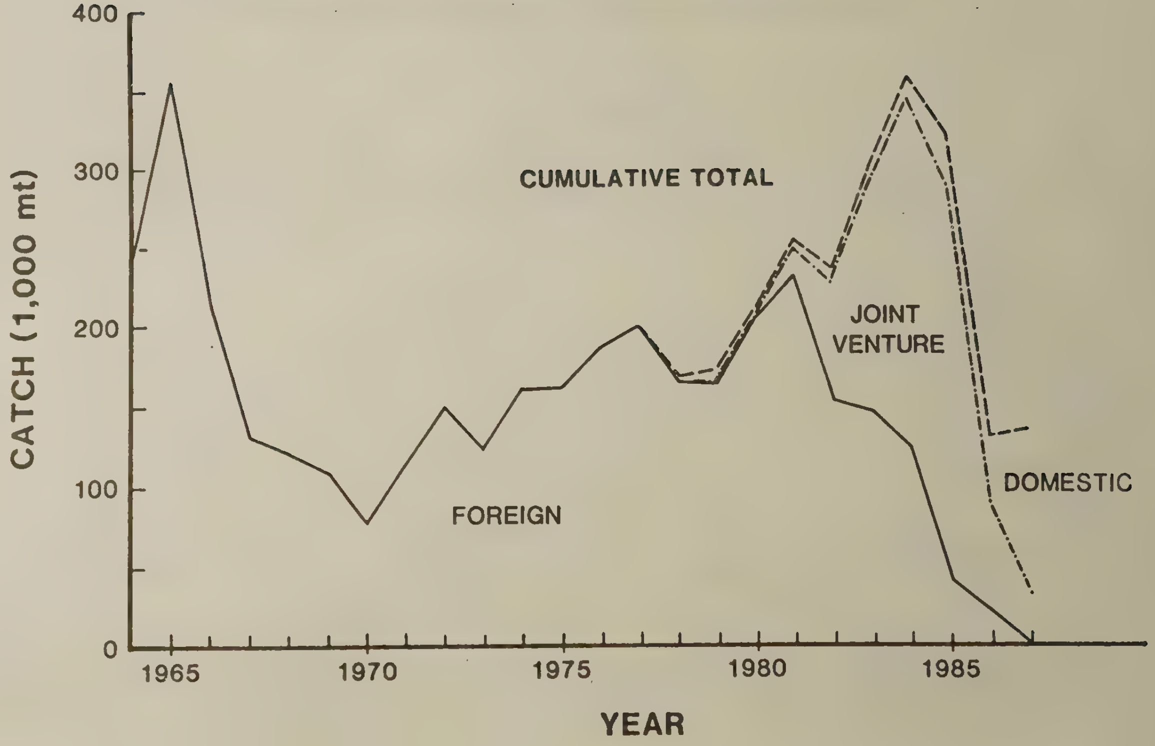


Figure 4. Annual groundfish harvests in the Gulf of Alaska.

Source: Major, R. L., ed. (1986); Smoker, J. E., personal communication.

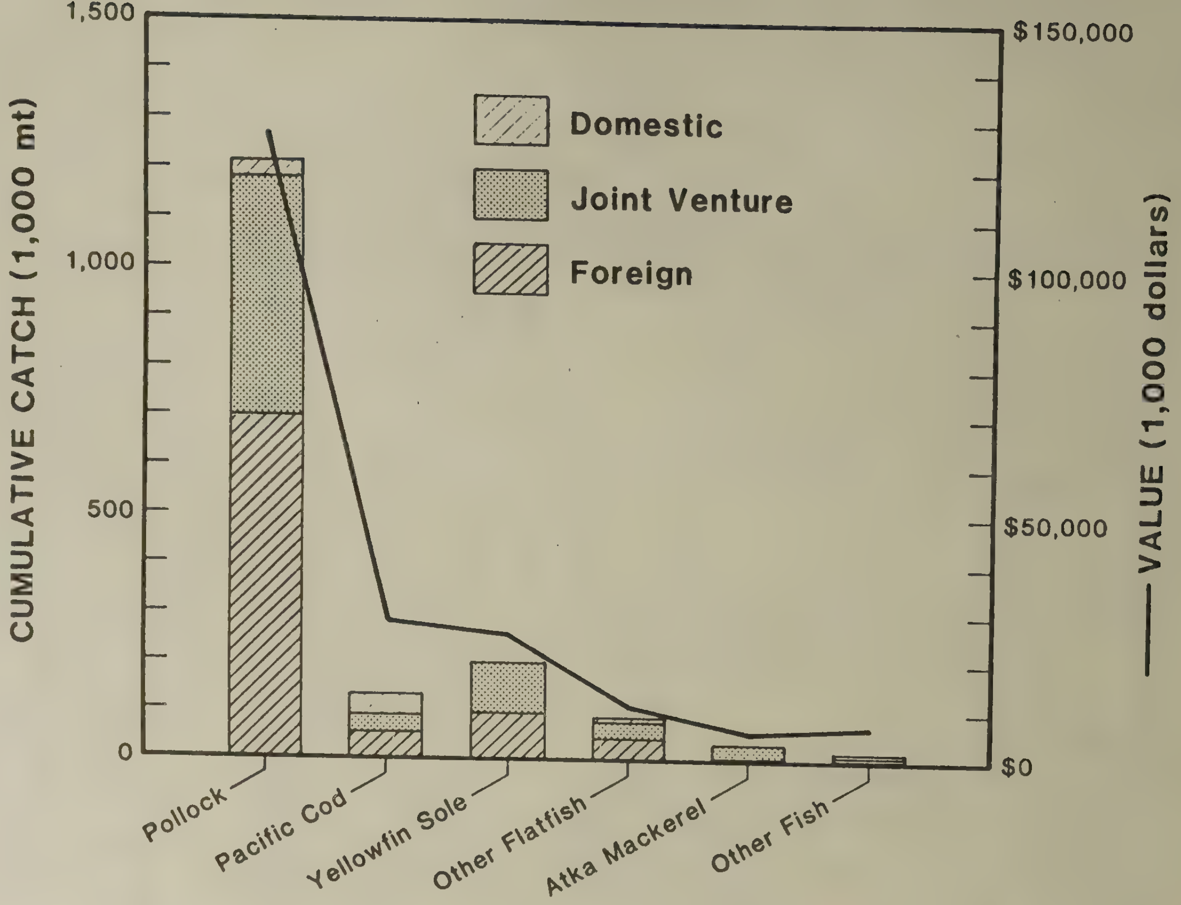


Figure 5. Average annual harvests, 1983-1985, and estimated exvessel value in the Bering Sea and Aleutian Islands.

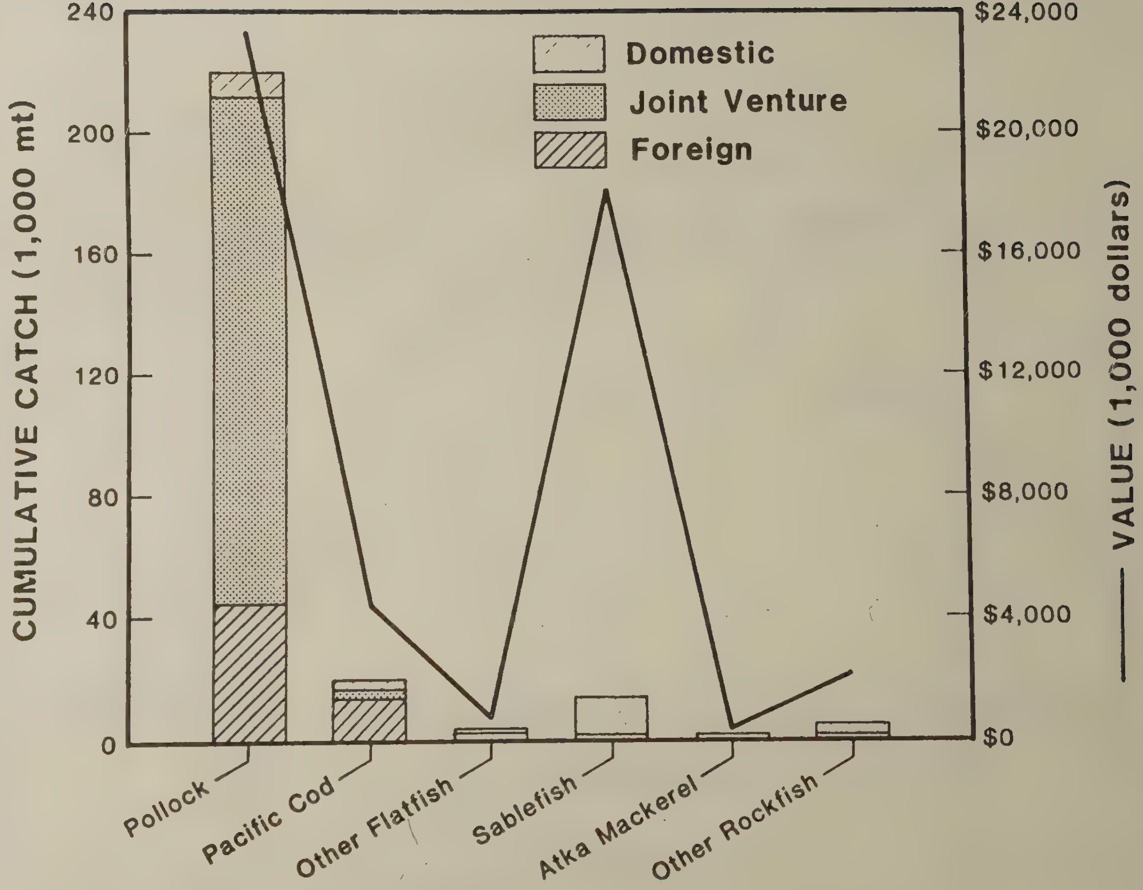


Figure 6. Average annual harvests, 1983-1985, and estimated exvessel value in the Gulf of Alaska.

Table 1. Acceptable biological catch (ABC) for groundfish species in the eastern Bering Sea, Aleutians, and Gulf of Alaska, 1988. Estimated value of unprocessed fish, assuming full utilization of ABC, and prices equal average of exvessel Alaska price and joint venture price.

| | ABC's Bering Sea & Aleutians | ABC's ABC's Gulf of Alaska | Total ABC's | Average unprocessed fish price | Estimated value of unprocessed fish |
|---|---|---|---|---|---|
| | metric tons | | | | $1,000's |
| Pollock | 1,660,000 | 225,000 | 1,885,000 | $ 105.2 | $198,231 |
| Pacific cod | 385,300 | 125,000 | 510,300 | 222.4 | 113,473 |
| YF Sole | 254,000 | 19,410 | 273,410 | 134.0 | 36,637 |
| Grlnd Turbot | 14,100 | 0 | 14,100 | 166.0 | 2,341 |
| A-T Flounder | 109,500 | 416,151 | 525,651 | 134.0 | 70,437 |
| Rock Sole | 183,885 | 117,416 | 301,302 | 159.2 | 47,980 |
| AK Plaice | 81,246 | 0 | 81,246 | 134.0 | 10,887 |
| Flathead Sole | 59,736 | 79,385 | 139,120 | 172.0 | 23,932 |
| Misc Flat | 7,033 | 135,337 | 142,370 | 134.0 | 19,078 |
| Sablefish | 12,200 | 35,000 | 47,200 | 1,322.4 | 62,417 |
| P-O-P | 22,600 | 3,300 | 25,900 | 319.6 | 8,277 |
| Rockfish | 1,500 | 16,800 | 18,300 | 491.5 | 8,994 |
| Atka Mack. | 21,000 | 0 | 21,000 | 151.0 | 3,171 |
| Thornyhead | 0 | 3,750 | 3,750 | 714.7 | 2,680 |
| Other Spec. | 54,000 | 10,312 | 64,312 | 130.9 | 8,418 |
| Totals | 2,866,100 | 1,186,862 | 4,052,962 | | $616,955 |

Sources:
(1) Summary for Industry Meeting, Extracted from Resource Assessment Document for Groundfish in the Bering Sea-Aleutian Islands as Assessed in 1987 and estimated Acceptable Biological Catch levels for 1988. December 3, 1987.
(2) Summary for Industry Meeting, extracted from Gulf of Alaska Groundfish Plan Team, Resource Assessment Document for Groundfish in the Gulf of Alaska. November 20, 1987.
(3) Prices are averaged from PACFIN reports for 1986 and joint venture prices reported by NMFS Alaska Regional Office.

## Management Under the MFCMA[2]

Two fishery management plans have been implemented to regulate fishing in the Gulf of Alaska and Bering Sea/Aleutians through a detailed set of conventional fishery regulations. The main features of these plans are as follows:

1. Optimum Yield (OY) and Total Allowable Catches (TAC): Each plan establishes a range for the OY for all groundfish species. In BSAI the range is 1.4 to 2.0 million metric tons, and in the GOA it is 116 to 800 thousand metric tons. The TAC for each species is determined each year based upon annual resource assessments; the TACs are adjusted so that the total for all species falls within the OY range.

Table 2. Estimated maximum annual value of groundfish products from harvest of Alaska groundfish.

| | ABCs for combined BSAI & GOA | Average product value per mt | Percent of ABC utilized | Estimated total product value ($1,000's) |
|---|---|---|---|---|
| Pollock | 1,885,000 | 478.84 | 100.00% | $902,620 |
| Pacific cod | 510,300 | 822.32 | 100.00% | 419,632 |
| YF Sole | 273,410 | 828.94 | 100.00% | 226,640 |
| Grlnd Turbot | 14,100 | 1,884.95 | 100.00% | 26,578 |
| A-T Flounder | 525,651 | 440.92 | 10.00% | 23,177 |
| Rock Sole | 301,302 | 828.94 | 100.00% | 249,760 |
| AK Plaice | 81,246 | 828.94 | 10.00% | 3,582 |
| Flathead Sole | 139,120 | 828.94 | 100.00% | 115,322 |
| Misc Flat | 142,370 | 828.94 | 50.00% | 55,320 |
| Sablefish | 47,200 | 1,886.33 | 100.00% | 89,035 |
| P-O-P | 25,900 | 1,242.30 | 100.00% | 32,176 |
| Rockfish | 18,300 | 1,242.30 | 100.00% | 22,734 |
| Atka Mack. | 21,000 | 661.39 | 100.00% | 13,889 |
| Thornyhead | 3,750 | 1,242.30 | 100.00% | 4,659 |
| Other Spec. | 64,312 | 661.39 | 50.00% | 21,268 |
| Totals | 4,052,962 | | | $2,206,391 |

Sources: Values per ton of harvested fish are based upon market prices for surimi, roe, shatter-pack fillets, headed and gutted frozen fish, and blocks; assumed distribution of raw fish to product categories; product yields derived from published documents and personal communications with industry members; and assumed partial utilization of arrowtooth flounder, Alaska plaice, miscellaneous flatfish and other species. Details of the calculation are available from the author on request.

2. Reserves and allocations: In BSAI 15% of each TAC is reserved, while none of the TAC in GOA is currently held in reserve. The non-reserved TACs are split between domestic annual harvest (DAH) and total allowable level of foreign fishing (TALFF) by allocating first to DAH all that the domestic fishing fleet is expected to harvest. The DAH is split between fishing for domestic processors (DAP) and joint venture processors (JVP), with domestic processors getting as much as they need before any TAC is allocated to JVP.
3. Season closures: The Alaska Regional Director of NMFS announces a closure for any species fishery when the directed (target) catch for that species to date plus expected incidental catch in fisheries for other species over the balance of the year reaches the TAC. When it is determined that the TAC is reached, the species is declared to be a prohibited species for the remainder of the year.
4. Prohibited species: Halibut, tanner crab, king crab, and salmon, as well as any species whose TAC has been reached, are considered prohibited species for trawl gear. These

species must be returned to the sea as soon after capture as practicable, and all fishermen are required to minimize their catches of prohibited species. The BSAI regulations directly establish prohibited species catch (PSC) limits, while the GOA regulations authorize the Regional Director to set PSC limits. For example, in Zone A of the BSAI (Figure 1) the limits are 80,000 tanner crab and 135,000 red king crab. For the entire BSAI the halibut PSC is 825,000 fish. When a PSC limit is reached, the bottom trawl fishery for yellowfin sole and "other flatfish" in Zone A is closed for the remainder of the year. After the PSC limit for halibut in the GOA is reached, the Regional Director prohibits fishing with trawl gear other than off-bottom trawls.

5. In-season adjustments: Both of the plans provide ample opportunity for the Regional Director to modify TACs, PSCs, closures, gear requirements, and allocations among DAP, JVP, and TALFF during the year. A series of specific considerations must justify these adjustments.
6. Time and area closures: In the Bering Sea the "Bristol Bay pot sanctuary" (area B, Figure 1) is closed to trawling, except that a portion of the area is open to trawl vessels participating in a special data-gathering program designed to measure incidental catch of prohibited species. Also, the "Winter halibut savings area" is closed to trawl vessels not having U.S. observers during December 1 through May 31 each year. In the GOA, directed fishing for sablefish with hook and line gear is closed from January 1 to March 31. Finally, four prime halibut fishing areas around Kodiak Island are closed to bottom trawling during all or part of the year. There have been other closures for foreign and domestic fishing not described here.
7. Gear limitations and allocations: Only trawls, hook and line gear, and fish pots are permitted to fish groundfish in the Gulf of Alaska; and fish pots are being phased out of the Gulf entirely by 1989. Sablefish is allocated primarily to hook and line gear fishing (80 percent in the central and western Gulf, and 95 percent in the eastern Gulf).
8. Observers: All vessels fishing in the EEZ of the Gulf of Alaska must take an observer on board when so requested by the Regional Director.

The foregoing regulations are reviewed and revised annually by the North Pacific Fishery Management Council and Department of Commerce to meet continually changing resource and economic conditions. The procedures for establishing annual TACs and PSCs, and the in-season adjustment mechanisms provide great flexibility in the regulations and assign a great deal of latitude to the Regional Director. This permits the Regional Director to respond to resource emergencies or other perceived problems in a relatively short time. In practice, the NPFMC is consulted before any significant management actions are taken.

## Conservation under the Management Plans

The multispecies Optimum Yields for BSAI and GOA, acting as overall groundfish harvest limits, are set at levels less than the sum of the MSYs for all species. Maintaining the OY at this moderate level forces the individual species quotas to be, at least on average, less than estimated annual biological yields. This does not, however, prevent overfishing of individual stocks or sub-stocks. TACs for Pacific cod and flatfish in the GOA have been set at low levels (relative to estimated MSYs) to control incidental catches of king crab and halibut and to retard the joint venture fishery. Even though stock dynamics depend upon exogenous natural fluctuations (e.g., in recruitment) and inter-species linkages (e.g., predation, and competition for food) as well as fishing mortality, this conservative approach to annual quotas provides substantial protection to the groundfish stocks managed by the FMPs.

As noted earlier, some non-target species in groundfish fisheries support extremely important commercial fisheries. As documented in the provisional foreign fishery observer data report (Clancy and Nelson, 1987), the joint venture vessels in the Bering Sea caught 262,200 king crab, 5,652,400 tanner crab, 602,200 halibut, and 20,700 salmon during 1986. Similarly, foreign fisheries caught 22,000 king crab; 1,518,000 tanner crab; 286,200 halibut; and 1,800 salmon. In each case, these catches are discarded with some mortality. Incidental catch regulations reflect conservation efforts for halibut, salmon, king crab, and tanner crab and indirect efforts to allocate economic benefits among the target fishing fleets.

Because discarding fish involves fishing mortality without fish landings, greater discards generally lead to lower stock sizes and allowable catches. For example, the International North Pacific Halibut Commission adjusts its annual harvest quota down by about 10 million pounds due to the incidental catch mortality. Some critics of the prohibited species policy note that the discard of unintentionally and unavoidably caught fish and crabs does not promote conservation of those species nor does it increase the economic benefits from the fishery. The opposing view notes that prohibited species status prevents potential targeting on these species by groundfish fleets, and prohibition is necessary to maintain species allocations based upon historical shares and to achieve optimum yield. Also, where incidental catches are predominantly small, fast-growing fish, the surviving discards will grow to make a valuable contribution to the target fishery. This latter view is strongly held by halibut managers. The extensive use of time and area closures, and the unusually low TACs for flatfish and cod in the Gulf of Alaska are partly a reflection of the prohibited species approach.

## Fleet Size, Processing Capacity and Overcapitalization

The rapid expansion of joint venture and domestic catch during the past seven years reflects the growth in fishing and processing capacity. The number of commercial fishing vessels receiving groundfish permits from NMFS's Alaska Regional Office has grown rapidly in every gear category (Figure 7).[3] From 1981 to 1987 the total number of groundfish permits grew from 199 to 1640, numbers of trawl gear permits grew from 54 to 197, and number of longline gear permits grew from 148 to 1435. Continuation of this trend will lead to excess capacity, or overcapitalization, in the fishing fleet.

Processing capacity is currently split between foreign and domestic. Overall, groundfish processing capacity is clearly greater than necessary, as evidenced by the early closure of the joint venture pollock fishery. Domestic processing capacity for species other than the traditional halibut and sablefish, however, is capable of handling only a fraction of the total groundfish caught. From the standpoint of U.S. policy which seeks economic development of the domestic industry, excessive multinational capacity for Alaska groundfish is not a concern.

An assessment of domestic groundfish capacity must distinguish between the separate trawl and longline fisheries, and it must recognize that at sea processing and fishing capacity are intimately linked in the factory trawl fishery. The halibut/sablefish longline fishery is a mature fishery which has already experienced widespread overcapitalization. Evidence for overcapitalization in the longline fishery is unambiguous. Between 1975 and 1986 the number of halibut fishing vessels grew by fifty percent, while the catching power per vessel at least doubled because of the switch from "J" hooks to circle hooks. Even though the halibut fishery is well managed for stock conservation, and annual halibut quotas remain at high levels, the fishing seasons are drastically reduced in length. In southeastern Alaska, the season length has dropped from 123 days in 1976 to three or four fishing days in 1986-87. In some areas halibut fishing was limited to twenty-four hour and twelve-hour openings, a practice that makes the fishery unsafe at times, and provides insufficient time for all fish to be properly dressed before being landed. Single day fishing capacity now exceeds the halibut quota in some areas, and the Director of the International Pacific Halibut Commission is prepared to recommend that trip limits be imposed upon halibut longliners.[4]

With short halibut seasons and high prices offered for sablefish, longline fishermen (especially those with vessels larger than 60 feet or so in length) increasingly diversify by switching to sablefish after halibut seasons are closed. The number of sablefish vessels grew by a factor of 7 from 1976 to 1987, with most of the growth coming after 1984. In the East Yakutat area the longline season lasted a full six months in 1984. It lasted only from April 1 to April 9 in 1987, despite the fact that the catch quota had been increased by fifty percent since 1984.

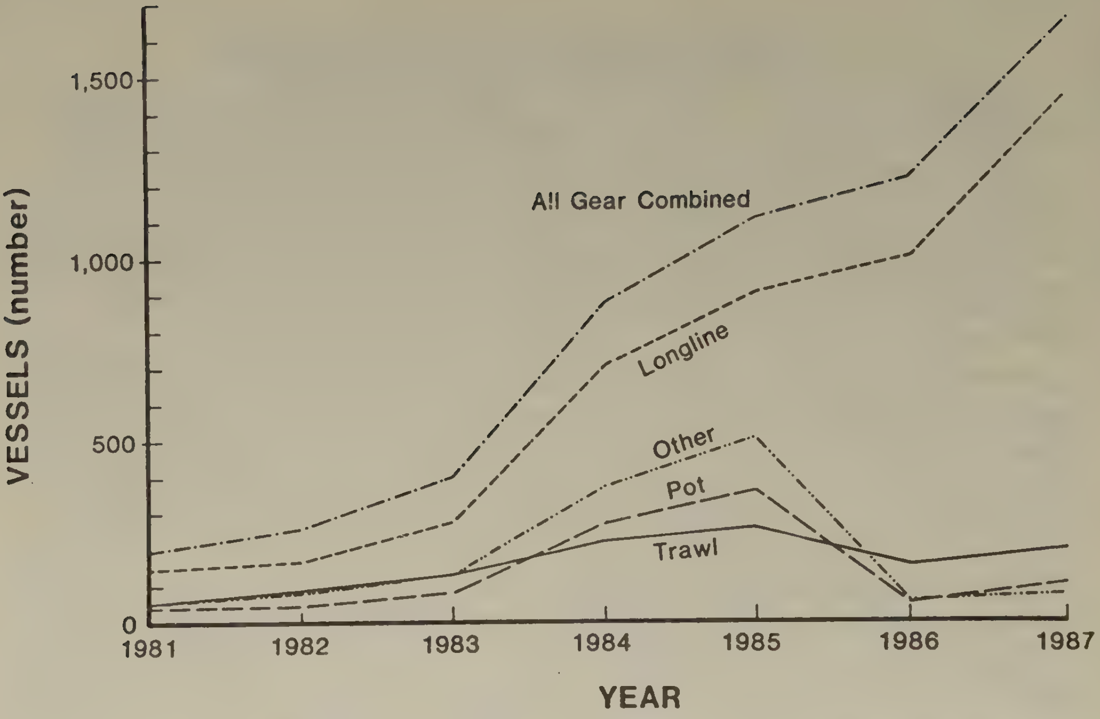


Figure 7. Number of groundfish permits issued by the National Marine Fisheries Service, Alaska Regional Office, Juneau.

As the domestic trawl fishery continues to expand, the evidence of excessive fishing capacity is emerging, but its effects are not yet strongly felt by major participants in the fishery. Shortened fishing seasons are one symptom. In the Bering Sea joint venture fishery, for example, the growing catch and fleet size has been accompanied by a progressively shorter season. During 1985 the JV harvest had reached 41 percent of its annual total by the end of April. During the comparable period of 1987, the catch reached 61 percent of the total, and the Bering Sea pollock quota had been reached before mid-June. Shorter fishing seasons in the joint venture fishery indicate that competition for pollock allocations has drawn excessive catching and processing capacity into the fishery. As noted above, most of the at-sea processing capacity is aboard foreign processing vessels. As U.S. processors begin to take a bigger share of the pollock, Pacific cod, and flatfish quotas, the same tendency to overcapacity may afflict the Americanized fishery.

While the existence of excess fishing capacity can be inferred from the progressively shorter fishing seasons, direct assessment of optimum capitalization for a fully domestic fishing and processing would be a more useful planning tool. This task is complicated by the technical diversity in fishing and processing operations, and because the capacity consistent with economic criteria depends upon fishing costs, catch rates, processing yields and costs, and the underlying biological constraints. All the factors determining the economic profitability of the fishery, in other words, need to be incorporated in the assessment of fishing capacity.

A practical approach to estimating optimal capacity must extrapolate from recent past experience and will invoke numerous simplifying assumptions. One method for doing this is the linear programming technique recently applied to multispecies groundfish fisheries on the Pacific coast (Huppert and Squires, 1987). Briefly, this is a mathematical method which finds the optimal (1) number of vessels, and (2) deployment of these vessels over areas and species. Optimal is defined as the maximum net economic return (total value of fish product minus cost of catching and processing) from the fishery, given the harvest quota constraints. The technique is called linear programming, because the objective is linear (a simple sum of profits from all segments of the fleet) and the constraints are linear (the sum of catches from all vessels must be less than or equal to the total allowable catch for each species).

The Appendix to this report contains a thorough description of a linear programming model developed for the Bering Sea and Aleutian Islands fishery. The model calculates the optimum fleet of factory trawlers and mothership operations for harvesting ABCs of pollock, Pacific cod, yellowfin sole, sablefish, Atka mackerel, other flatfish, rockfish, and other groundfish. Five classes of fishing operation are included; small, medium and large factory trawlers, small and large motherships.[5] Given the harvest quota constraints, the linear program selects the number of vessels in each class, and the deployment of those vessels (defined as assignments of available fishing and processing days among areas and target fishing strategies), to maximize net economic benefit from the fishery.

Fishing and processing costs, catch rates, and prices assumed for the calculation are discussed in the Appendix. Biological constraints on total annual harvests are represented by the recently recommended ABCs for 1988. Using these basic assumptions, the optimum fleet for Bering Sea and Aleutian Islands groundfish would contain 3 medium factory trawlers, 21 large factory trawlers, and 6 fillet motherships, and 3 large surimi motherships. Between 44 and 50 catcher vessels would supply the motherships. The projected total economic profit (over and above an assumed 10 percent return on capital investment) from this operation would be around $124 million per year, representing the total fish product value minus costs of harvesting and processing at-sea.

The optimum fleet estimated from this base calculation is surprisingly small considering that 140 motherships participated in the Bering Sea joint venture fishery in 1986 (Clancy and Nelson, 1987). One reason for this incongruity is that joint venture motherships fished an average of only 70 days in 1986, while full capacity utilization is assumed to be 265 fishing days per year for motherships. Also, an unknown fraction of the motherships operating in 1986 may have been smaller than the 460-foot motherships included in the model. Medium factory trawlers are assumed to be capable of fishing 260 days per year, but similar trawlers in the foreign fishery in 1986 fished an average of only about 40 days. Thus, a full-time factory trawler/mothership fleet operating at capacity in the Bering sea need not be nearly as large as recent foreign fleets.

Another surprise is that small freezer trawlers were not a significant part of the optimum fleet. In recent years, small freezer trawlers, used for producing headed and gutted fish and pollock/cod fillets, were a major component of the growing domestic trawler fleet. Three reasons for the divergence between model results and actual economic development patterns are apparent. First, the model does not include a financial constraint to reflect the difficulty fishing companies may have in raising the substantial capital needed for larger ships. Second, many of the small trawlers are designed to operate in the Gulf of Alaska fisheries where large scale pollock processing is less important than in the BSAI. Third, the economic returns predicted by the model presumes, as noted above, that an efficiently planned fleet operates during the entire fishing season. Under the existing "Olympic system" (i.e., open access competition), no rational investor would make this assumption, and the actual pattern of investments will reflect this reality.

A variety of practical considerations can be inserted into the economic model by changing the constraints, or by modifying assumed cost, price, or product yield rates. Some of these changes are examined in the Appendix. For example, an optimum fleet with large motherships excluded, would consist primarily of large factory trawlers generating a total net economic return of $97.8 million per year ($26.3 million less than the base calculations). Other calculations show that the trawl fleet would become largely unprofitable with 20 percent lower fish prices, and that aggregate fleet profits could increase to $281 million per year if prices rise by 20 percent.

These computations are useful guides to efficient fleet size, and they estimate the potential economic return which is likely to be squandered by overcapitalization under open access. Although the existing domestic catcher/processor fleet is not too large by this standard, there are currently far more than the requisite catcher vessels in the joint venture fishery. And, under the existing management system the fleet cannot be expected to stop growing when it reaches the optimum size.

## Current Management Problems

Several problems in the Alaska groundfish system are apparent from the above discussion. It is increasingly evident that rapid growth in the domestic fishing fleet will soon prevent the United States from achieving economic efficiency objectives. Accompanying that growth, extensive waste of incidentally caught and discarded crab and halibut will be a concern. Until an adequate domestic observer program is established, the decreasing volume of catch sampling and fishery monitoring that attends the Americanization of the fishery is a threat to the credibility of scientific stock assessments. With little prospect of additional Federal funding from general tax revenues for regulation and monitoring, the Council's inability to collect resource rents from commercial harvesters may curtail necessary management and research activities. Evaluation of new management approaches for dealing with the emerging fishery problems requires careful consideration of objectives of public fishery management.

## Notes to Section II

1. Prices, product yields, and allocations of harvested quantities among product categories for this computation are the same as those assumed for the optimum fleet calculations described in the Appendix to this report.
2. The descriptions of the management system and associated regulations are derived from recent versions of the two plans (NPFMC, 1984, 1986), the 1987 Gulf of Alaska groundfish regulations, and a draft of the Bering Sea and Aleutian Islands Area regulations (Code of Federal Regulations, Title 50, Parts 672 and 675).
3. These permits are required of all vessels fishing for groundfish in the EEZ. They are provided to all applicants, and are used for monitoring and record-keeping. They do not limit the entry of vessels to the fishery.
4. See the Opinion in the November, 1987 issue of Pacific Fishing magazine (p. 154).
5. The absence of shoreside processing plants from the model represents a data deficiency, not a finding that shoreside processing in Dutch Harbor, Akutan, Kodiak, and other areas cannot handle a significant portion of the groundfish in the Bering Sea.

# III. Objectives

To choose a rational course of action requires knowledge of options, prediction of consequences, and awareness of objectives. Because they derive from conflicting interests and ideologies among fishery management agencies and industry groups, stated fishery management objectives are frequently overlapping, vague, or contradictory. To evaluate management options logically, it is necessary to choose a limited number of objectives. Such a choice requires rejection of some objectives; hence, a diminished attention to the interests of someone. Because this report is concerned with the overall performance of the commercial fisheries, and not with particular commercial interests, it will focus on broad, public policy objectives. The management objectives adopted here are distilled from the Magnuson Fishery Conservation and Management Act (MFCMA), the North Pacific Fishery Management Council's "Comprehensive Fishery Management Goals," management plans developed for groundfish fisheries, and other public expressions of resource management policy.

## Fish Stock Conservation

A first criterion is that fish stocks be maintained at levels that permit large annual harvests and prevent overfishing. Past and current efforts by NMFS and NPFMC have emphasized annual yield estimates based upon scientific assessments fish abundance and research on key biological parameters. Fishery regulations include quotas to assure that annual harvest remain within acceptable bounds. Because the current regulations and any foreseeable modified regulations are likely to assure conservation of the major fish stocks, this report does not critically examine nor recommend modifications to the procedures adopted for assessing stock abundances and determining sustainable yields.

Because fish stocks fluctuate, a long run sustainable yield concept, like MSY, is inappropriate for assigning annual allowable catches. The Allowable Biological Catch (ABC) concept is a more flexible guide to annual quotas as it recognizes the fact that fish stocks vary, sometimes erratically, through time.[1] The Scientific and Statistical Committee (SSC) of the NPFMC has adopted a pragmatic definition which makes ABC a quantity that is above or below MSY as the underlying fish stock is greater or smaller than the level needed to sustain MSY. Multiplying the MSY fishing mortality rate times the current biomass provides a useful rule-of-thumb for calculating the appropriate quantity. The ABCs have not been calculated based upon the SSC's new definition as of yet. The management Teams have used similar approaches, some involving application of constant rates of exploitation to stock biomass. Whatever formal mechanism is used, annual adjustment of harvest levels is demanded of a management program under this resource conservation criterion.

While existing FMPs appear capable of conserving fish stocks, ambiguities and uncertainties regarding stocks and biological productivities may diminish the effectiveness of the conservation effort. For example, pollock populations in the Bering sea may sub-divide into several "stocks."[2] Different, but equally plausible, delineations of stock boundaries will lead to different estimates of potential yield in the EEZ. This source of ambiguity in scientific guidance on annual allowable catches adds to the substantial uncertainty in stock abundance due to wide variances in statistical estimates. Another problem is unknown volume of discards. Lack of information on quantities of fish discarded at sea poses a problem for stock assessment based on catch-per-effort. Unless on-site monitoring or accurate extrapolation from samples provide estimates of discard mortality, fishing mortality will be under-estimated. This latter is not a significant problem for stock assessments so long as fish stocks are monitored through fishery-independent surveys.

## Economic Benefits

Economic benefits are commonly measured as the fishery's contribution to net income; that is, value of fishery products minus cost of production. The product value is expressed as the value to consumers, and the costs include all costs from harvesting, through processing and distribution, to retail marketing. Obtaining maximum economic benefits from a fishery depends upon several inter-related sub-objectives: (1) economic efficiency in harvesting and processing of fish; (2) producing and marketing an optimum mix of seafood products; (3) assuring product quality; and (4) technical innovation and productivity improvement through time in both harvesting and processing. These objectives, common to economic appraisals of industry performance throughout the economy, are achieved largely through private competition in fish product markets. Fishery management deals almost exclusively with sub-objective (1), which is not achieved through private competitive processes so long as the fish stocks remain open access resources.

It is useful to decompose the economic efficiency criterion further. First, efficient production requires a fleet of fishing vessels having sufficient capacity to harvest those fish worth harvesting on a cost-effective seasonal schedule. Because catch rates vary, and annual allowable catches fluctuate, the ideal harvest capacity will be capable of taking somewhat more than the average annual total allowable catches. Second, fish processing capacity should be matched to overall harvest capacity and it should be designed to produce the most valuable mix of products. Third, the cost of collecting scientific information, assessing fish stocks, monitoring catches and fishing effort, and enforcing fishing regulation should not be excessive. While optimal enforcement and monitoring effort cannot be precisely defined, specific features of the fishery management system should be evaluated for cost as well as resource conservation consequences.

In practice economic benefits from efficient production can be calculated at a regional, a national, or an international level of aggregation. While a national accounting stance is consistent with the National Standards of the MFCMA, regional interest groups will not be equally served by a national benefits objective. Maximizing national benefits may conflict with regional economic objectives whenever efficient production requires a shift in regional concentrations of economic activity.[3] When economic activity declines in a region, this normally results in reduced income to owners of immobile assets (land, buildings, harbors, etc.) for which demand has fallen. Thus, leaders of communities threatened with a loss of economic base (due to private business decisions, government regulations or whatever) will oppose a shift in economic activity even if the shift is consistent with maximizing benefits to the nation. In an important way, therefore, the national economic benefits objective may conflict with a regional economic objective.

## Maintaining Flexibility

This objective overlaps both of the previous objectives, but is important enough to be stated separately. The recent history of fishing in Alaska provides abundant evidence that biological and economic changes can occur rapidly and unpredictably. To remain profitable over the long term, fishing firms must be adaptable to changing resources and markets. Diversification of fishing operations may be a part of this flexibility. Combination vessels are constructed with the expectation that during their useful lives they may be transferred among several distinct fisheries. A good example is the king crab/trawler combination. A substantial portion of the 125-vessel joint venture midwater trawl fleet came from the king crab fishery. Fishery regulations may preserve opportunities for fishing businesses to adapt and change as conditions change.

A similar objective is to design flexibility into key management procedures. New information, or developments in technology, may make established catch quotas or allocations illogical at a later date. For example, managers may need to designate a fish species as prohibited catch, while reserving the option to remove that designation when necessary. It should be possible to combine or separate individual species in quota regulations as appropriate for given circumstances. To maintain flexibility, managers should avoid getting boxed into a specific allocation of fish to narrowly defined gear groups or seasons or areas.

## An Equitable Distribution of Fishery Benefits

Any set of management regulations will result in a distinct distribution of economic benefits. No generally accepted notion of fair and equitable treatment is available for judging equity of a given distribution among user groups or between resource users and the public at large. Nevertheless, there are specific approaches to equity that provide some logical guidance.

Fairness may be gauged either by outcomes (e.g., number of fish caught or income earned) or by processes (e.g., fair competition, or rules for entry). For example, judging on the basis of outcomes, it may be deemed unfair for a single fisherman or fishing company to harvest a preponderance of the catch, or to earn a preponderance of the profit. On the other hand, judging on the basis of process, a particular share may be fair or unfair depending upon whether the management system gives everyone an opportunity to harvest or earn profit. Where the outcome is the result of fair competition, and shares correlate with skill and planning, even a grossly unequal division of benefits may be considered equitable. To be useful guides to policy, notions of equity cannot be left ambiguous or fuzzy. Successful application of this criterion requires conscious adoption of explicit standards.

One standard is the prohibition of specific objectionable practices. For example, the MFCMA prohibits discriminating among U.S. citizens based upon State of residence. Equity may also require that any single fishing firm be prevented from dominating a fishery. These would be minimum standards for any regulation.

In evaluating a regulatory change, another useful approach to achieving equity is to avoid creating economic "losers" (e.g., anyone whose resource access or income-earning ability is significantly diminished).[4] Where fish catch is a reasonable proxy for benefits, approximate equity among user groups may be attained by maintaining catch shares. In a fishery that is developing as rapidly as the north Pacific groundfish fishery, however, simple guides, like past shares, need to be augmented to deal with change. Equity could be judged by fair process: concepts such as fair compensation,[5] or equal access to resources, or the fairness of the competition in which fish or economic benefits are obtained. Equity in dealing with user groups will be especially poignant issue in developing limited access programs, where government is seen as directly involved in the distribution of benefits.

As noted in the discussion of economic benefits, a management action that improves overall economic benefits can cause a loss in economic benefits in one location while increasing benefits in another location. Inter-regional shifts in economic benefits represent a most difficult problem for the "no losers" standard of equity. Because regional shifts in fishing and processing activity accompany almost any management action (especially limiting access), a strict version of the no losers criterion will prevent any action. A weaker version of the standard, such as "no significant uncompensated losers," is consistent with actual management practice.

Another question of equity concerns the division of costs and benefits between the commercial fishery and the public at large. On this subject, the President of the American Fisheries Society recently stated

> "It is a commonly accepted concept that those who use our resources should be charged a fair rate of rent to pay the cost for management, research, rehabilitation, and enhancement of the resource. Our present system of open entry fisheries and low-to-no user fees . . . causes the consumer to pay a higher price for a lower quality product. The loser is the owner of the resource, the public."[6]

The standard that firms should pay for using public resources is applied in some circumstances and not in others. Royalties paid by oil producers on Alaska's north slope, for example, represent an acceptable transfer of wealth from oil companies to the public. Timber sales from national forests are similar, but are sometimes made "below cost." Public irrigation projects in arid western States rarely, if ever, charge full costs to water recipients. There is no precedent for charging resource management costs to marine fisheries. Consequently, public resource policy is clearly inconsistent regarding distribution of benefits and costs between resource users and taxpayers.

The MFCMA establishes the national ownership and authority for managing fishery resources in the Exclusive Economic Zone (EEZ), but it is ambiguous regarding the extent to which users should pay for taking fish.[7] The law does not designate what share of the fishery benefits should accrue to the general public versus the fishing industry. Hence, the distribution of benefits between public and private interests warrants careful examination in developing management alternatives.

## Optimum Yield

The MCFMA defines optimum yield (OY) as the quantity of fish prescribed on the basis of MSY as modified by any relevant economic, social, or ecological factor. An alternate definition of OY is the annual harvest that produces the largest benefits to the nation as a whole. This concept is not separate from the foregoing objectives; it incorporates all those other elements. OY involves a balancing of various objectives or criteria. For example, neither maximizing catch nor maximizing economic return would necessarily optimize the fishery. An optimum yield is the best balance of conservation, economic benefit, equity and flexibility.

## Conclusion

In summary, groundfish management should be evaluated with respect to (1) fish stock conservation, (2) level of net economic benefits, (3) flexibility for management and private industry actions, and (4) equity in distributing economic benefits. If these objectives are adequately addressed, the "optimum yield" standard will be readily accomplished as well. Constraints on achievement of these objectives include political and administrative feasibility, consistency with national fishery policy, and scientific knowledge. Rational formulation of management regulations requires selection from among the feasible alternatives based upon the management objectives. While this rational model of decision-making is often attacked as unrealistic in detail, it provides a useful framework for examining improvements in the groundfish management regime.

## Endnotes to Section III

1. The crash in king crab abundance in the early 1980s, the unanticipated resurgence in Pacific halibut in recent years, and the pollock disappearance from the Shelikof Strait two years ago provide ready examples of rapidly changing stocks.

2. It is currently unclear, for example, whether the pollock in the Bering sea between U.S. and Soviet 200-mile zones (the so-called "donut hole") belongs to the stock inhabiting the U.S. zone.

3. Program analysts recognize the economic importance, hence political importance, of "secondary benefits," regional increases in employment and income beyond those occurring in the primary industry. These secondary benefits tend to be balanced by equivalent losses elsewhere. Income-producing primary production activities, like fishing, will attract both support industries (ship repair, gear suppliers, fuel docks, grocery stores, etc.) and businesses related to use of the primary output (i.e., fish processors, brokers, cold storage facilities, shipping companies, etc.). Wherever the fish harvesting industry locates, these ancillary activities will also concentrate. As long as this is somewhere in the nation, the national economic benefits are essentially independent of location.

   Conflicts arise, however, when a region seeks to increase its secondary benefits at the expense of another region by, for example, moving a fishing fleet from one port to another. If the new port is better located and results in lower shipping or vessel transportation costs, then greater national economic benefits (measured by the reduced costs) will accompany the shift of the fleet to a new location. Local businesses and landowners in the new location are likely to gain economic benefits from shifting the fleet to their neighborhood even if there are no net national economic benefits. The business community at the old location will lose approximately an equal amount. Thus each region will want to establish the primary industry in their region regardless of whether their's is the best location.

   To a large extent, regional rivalries over location of economic activities amount to contests for secondary benefits that cancel out in the aggregate (i.e., it is a zero-sum game). Transfers of wealth through competition for industries are not justified by the national economic criterion. Such transfers of wealth may be justified on other grounds, such as a need to maintain incomes in isolated communities. This aspect of economic benefits falls within the equity objective discussed below.

4. The "no losers" criterion is equivalent to the concept of "Pareto optimality." A particular allocation of resources is termed optimal only if no one can be made better off without making someone else worse off. When applied to a change in allocation, this implies that at least one person is made better off while no one is worse off. This is clearly a very weak criterion in that everyone may be badly off even with an optimal allocation. The strength of this concept is that it requires no explicit weighing of different individual's welfare.

5. The question of what constitutes fair compensation for loss of property, for personal injury, and for taking of rights or privileges has long been a subject of judicial action. Courts make decisions in specific cases. But we do not expect these settlements to provide useful guidance to fairness in compensating fishermen for management actions that harm them. Fair compensation can be technically defined as an amount of money sufficiently large to satisfy the recipient (e.g., an amount equal to income lost). Whether the recipient is actually entitled to this compensation depends upon the property rights, or rules of access, prevalent in the fishery. Generally speaking, fishermen do not have rights to income from fish resource, and they cannot sue for compensation of losses attributed to management actions. It is conceivable, however, that a limited access system could establish such rights.

6. S.A. Moberly. 1977. President's Corner. Fisheries. 12(5):39. The concern over fish quality and price in this statement is not especially pertinent to Alaska groundfish. Most of the

groundfish products are of increasingly high quality and consumer prices have not been raised due to excessive competition in the fishery.

7. In a detailed legal interpretation of the MFCMA, W. T. Burke (1977) concludes that the Act does not prevent the collection of substantial taxes and fees from fishermen. Most other interpretations, including that of the General Counsel for the National Marine Fisheries Service, focus on the statement in section 304(d) of the Act that requires fees charged for fishing permits not to exceed the administrative costs incurred in issuing the permits. This statement suggests no rent can be collected by the Federal government.

## IV. Conventional Regulations

All the regulations currently used in Alaska groundfish management can be classified as "conventional." They restrict the commercial fisherman's choice of fishing gear, timing, area or species. Conventional regulations work to defeat the consequences of open competition for fish; they do not alter the institutions and property rights arrangements that make commercial profit incentives conflict with resource conservation. These regulations, in effect, treat symptoms rather than fundamental causes of conservation failures in the fishery.

Treatment of symptoms can be effective; and conventional regulations are frequently successful in maintaining fish abundance. Assuming that groundfish management must continue to rely heavily upon conventional regulations, it is important to consider modifications that may help to more fully achieve fishery management objectives. The regulatory options discussed below include some likely candidates for change. In light of the declining foreign fishery, only regulations applied to domestic fishing operations (joint venture, factory trawler, and shoreside delivery) are considered.

### Regional Division of Species Quotas

Quotas are subdivided to protect sub-stocks, to extend fishing seasons, and to allocate harvest shares among fishing fleets or processing plants in various locations. Similarly, multiple season openings and closures in a given area can spread the harvest over different fishing fleets, and they can help to separate in time various incompatible uses of the fishing grounds. As noted in Section II above, the current Groundfish FMPs include a wide variety of techniques of this sort. For example:

1. Quotas are completely separated between Bering Sea and Gulf of Alaska. This is both an administrative division (the two FMPs require separate harvest quotas) and a division of biologically separate populations.
2. In the Gulf of Alaska the target quotas for sablefish are allocated into Southeastern, central and western sub-areas.

Where there are separable stocks of fish, in the sense that one stock is largely unaffected by level of harvest on other stocks, the corresponding separation of harvest quotas facilitates maximizing overall average annual yields. This addresses the fish stock conservation objective, while it does not interfere with achievement of economic benefits and equity. No further sub-divisions are proposed or recommended by this report.

## Allocation of Quotas among Gear Types

Two main reasons for prohibiting a particular gear or restricting catch by gear type are (1) to increase the total physical yield from a stock and (2) to establish by regulation the distribution of economic benefits among groups of fishermen. The physical yield objective is exemplified in the prohibition of trawl gear in the halibut fishery, and by the special fishing grounds and seasons reserved for non-trawl fishing. The second motive is evident in the Gulf of Alaska groundfish regulations that divide up sablefish quotas among longline, trawl, and pot gear.

## Incidental and Prohibited Species Catch Regulations

Prohibited species catch limits play an important role in regulating the groundfish fishery, because (1) they represent an administrative procedure for separating fisheries by gear type, and (2) they provide a mechanism for allowing multi-species fisheries to continue after one species' harvest quota has been reached. As noted in Section II, trawlers are prohibited from retaining high-valued species like halibut, king and tanner crab, and salmon. Also, after a particular groundfish species quota is exhausted in any regulated area, that species becomes a prohibited species during the remainder of the year in that area.

A significant problem encountered under the existing prohibited species regulation, is that substantial portions of the incidental harvests are discarded dead. This clearly reduces the economic benefits from what they would be if fishing methods did not capture prohibited species. To eliminate the mortality of discarded fish is not technically possible, however, so the economic objective requires establishing a method of balancing benefits of prohibiting landings with costs of discarding. A second problem is that when large volumes of discards are not recorded, uncertainty regarding fishing mortality rates reduces the accuracy of the stock assessments and annual biological yield estimates.

In the case of halibut and sablefish, for example, the extremely short halibut season induces fishermen to discard essentially all species except halibut during halibut fishing. Similarly, as the sablefish fishing season was shortened to a few days, the fishermen specialized in landing only sablefish while discarding all other species (including the prohibited halibut). Requiring fishermen to land single species during each specialized season is generally inefficient and wasteful. Fortunately, the longline fishermen are often able to target with fair precision, thus limiting the total mortality due to discards.

One promising modification to the prohibited species regulation, proposed by a NPFMC member, would reallocate some of the species quotas from the target fishery to non-target fisheries. Instead of discarding all halibut during the sablefish season, for example, one could allow halibut to be landed as a proportion of sablefish landings (10% of sablefish, for example). A different proportion for halibut might be permitted in Pacific cod landings. Given the allowable incidental catch, the managers could calculate the quantity of halibut likely to be landed in the sablefish and/or cod fishery. This quantity would then be subtracted from the target halibut quota during the open halibut season. Extension of this concept to other species and gear types could be pursued.

If incidental harvests legalized by this procedure would otherwise have been discarded dead, the total harvest will be increased and clear economic gains can be enjoyed. Also, where two species can be caught by the same gear in the same area, the overall costs of catching both together will generally be lower than costs of catching the two separately. If harvests can be increased while overall fishing costs are decreased, the economic efficiency gains from this approach can be substantial. The potential economic gain must be weighed against the possibility that legalization of landings by a new gear, or in combination with a another species, may induce fishermen to modify fishing tactics such that total discards actually increase.

Regardless of the potential for overall economic gains, the re-allocation of high-priced species like halibut and sablefish from intense, directed fishing seasons, to multispecies fisheries will meet substantial opposition. The change to multispecies fishing would disadvantage those fishermen whose fishing strategies are well adapted only to the short, intense, single-species fishing season.

Analysis of the options here is difficult due to well known problems in data gathering. Solid evidence regarding discards, and, more importantly, prospective discards under hypothetical conditions, are not available. Consequently it is not possible to determine whether potential cost savings and harvest increases through multispecies fishing will be significant.

## Limit the Catch per Trip

The so-called "trip limit" is intended to reduce the rate of harvest (landings per week) during an open fishing season in order to increase the length of the season. The tactic can be successfully applied to shore-based fishing if the fishing vessels are unable to increase the frequency of trips to compensate for reduced catch per trip. Trip limits are not used in Alaskan groundfish fisheries yet, but the Director of the International Pacific Halibut Commission has expressed an interest in using trip limits in the future. Examination of the experience with trip limits on the west coast should prove instructive.

In response to the Pacific Fishery Management Council's 30,000 pound trip limit on widow rockfish, many trawlers reduced fishing trip length and increased trip frequency. The Council responded by limiting the allowable trip frequency to once per week. When the trip limit was reduced to 20,000 pounds, some of the larger midwater trawl vessels could no longer cover operating costs. To redress this unequal impact three options were offered each fishing vessel: a once per week limit of 20,000 pounds; a once per two week limit of 40,000 pounds; and a twice per week limit of 10,000 pounds.

Trip limit regulation has been fairly successful in spreading out widow rockfish harvests over a longer period of time, an effect that purportedly helps to sustain rockfish fillet markets and to improve the economic returns to the groundfish processing/marketing sector. In 1986, the PFMC imposed trip limits for widow rockfish, other rockfish (the Sebastes complex), and for sablefish. The Sebastes complex trip limit in August of 1986 permitted vessels north of Coos Bay, Oregon to land weekly 30,000 pound of Sebastes of which no more than 12,500 pounds could be yellowtail rockfish. Sablefish trip limits for trawl gear was set at 8,000 pounds (no limit for longline and pot gear), and a maximum of 5,000 pound per trip are allowed to be smaller than 22 inches in length. Some trawl captains delivering loads of mixed species while subject to all of these numerical limits found that they often had to discard an excessive amount of fish or risk running afoul of one of the limits.

Thus, when applied to several species in a mixed species fishery, a significant weakness is exposed—that trip limits assume fishermen have precise control over the mix of species caught. High discards of desirable species do not promote economic efficiency, stock conservation, or flexibility. Rigid numerical quotas for specific trips or short time periods do not recommend themselves for trawl fisheries. Still, trip limits may be useful in lengthening the season openings and in improving the product quality in extremely crowded, single-species fisheries like that for the Pacific halibut.

## Conclusions

Conventional approaches to fishery regulation have an important role to play in the achievement of management objectives. They can assure that fish stocks are not overfished; that fishing is tailored to regions and substocks; that patterns of fishing mortality conform to age-class, size, and species compositions maximizing physical yield; and that fish catches are allocated to groups of fishermen with historical or other claims on the fishery.

Conventional regulations also cause unintended, and often undesired, reallocations of harvest shares among segments of the fishing fleet. They do not maximize overall economic benefits of commercial fishing, because they encourage excess fishing capacity, overcapitalization, and short fishing seasons. The prevalence of short, congested fishing seasons in high-valued fisheries under quota regulation (e.g., Pacific halibut, sablefish, west coast salmon), may cause unbalanced fishing on various sub-stocks, resulting in sub-optimal biological yields. Modifying prohibited species regulations to permit some legal harvest of by-catches, and setting trip limits to slow down the rate of landings, however, could improve the utilization of high-valued species, like halibut, that are subject to excessive fishing pressure.

## V. Limited Access—Options and Program Elements

Limited access systems vary widely in detail, but they share a common trait. They deal directly with the underlying cause of excess fishing capacity in open access fisheries, by replacing open access to fish stocks with clearly allocated fishing rights. Under favorable circumstances, any of the common variants—license limitation, allocation of individual fishing quotas, or assignment of full property rights—can significantly improve the management of fisheries. Whether a particular implementation secures significant economic benefits, satisfies objectives of equity, and promotes fish stock conservation will depend upon the specific program design and the particular implementation. Extensive experience in Alaska, Canada, Australia, New Zealand, and elsewhere clearly demonstrates that management objectives can be addressed by limiting access, and that there are predictable pitfalls.[1] The following discussion describes and evaluates various options that might be considered in Alaska groundfish.

### The Range of Options

There are basically four options for limited access: license limitation, individual quotas, full private property rights, and full public enterprise operation of the fishery.[2] The first two of these are given most serious attention, while discussion of the latter two serves to place the other two in perspective.

License limitation, the most widely used limited access method, restricts fishing rights to a group of identified license holders. Most licensing systems give licensees co-equal rights to harvest. Some licensing program deviate from co-equal rights by creating special classes of license holders.[3] No specific quantity of fish is assigned to licenses, but a wide variety of ancillary restrictions on gear, area, timing, and species may be attached to licenses.

Individual quotas assign specific quantities of annual harvest rights to each harvester. The total allowable catch for a given stock or for several inter-related stocks, may be divided up among individual quotas. Two principal alternatives for individual quotas are fixed quantitative rights (e.g., a right to harvest 10 tons of sablefish) and annually variable share quotas (e.g., a right to harvest 1 percent of the total allowable catch). Several different versions of individual quotas go by the names "individual fisherman quota" (IFQ), "individual tradeable quota" (ITQ), "enterprise allocation," and "share quota."

Full private property rights would mean ownership of fish stocks by individuals, corporations, or other entities. The resource owners would have the full range of rights and responsibilities accorded owners of land-based resources, and they would harvest from the stocks in accordance with their own objectives and capabilities. Fish stock owners would be responsible for stock assessment, harvesting, and sale of fish. They would have access to the judicial system for redress of damages to their property (e.g., to seek compensation for unauthorized harvesting), and they could petition for public policing to prevent trespass and injury to their stocks. This option is not given much attention for two principal reasons: (1) it is difficult to establish and enforce ownership to fugitive fish in the ocean, and (2) long tradition and existing laws would have to be drastically revised to permit private ownership of marine fish.[4]

A public enterprise in a marine fishery would operate like a private resource owner. The public enterprise would eliminate open access competition for fish by hiring its own fishing vessels or by contracting with private harvesters to catch annual quotas. Fishing contracts, like contracts to build roads or to dredge harbors, could be issued on a competitive basis. Each fishing contract would stipulate a quantity, species or mix of species, fish condition, fishing time, and landing location. The public enterprise would supply fish to the market at a fair price. Like irrigation water or electric power provided by public enterprise agencies (e.g., Bureau or Reclamation or Bonneville Power Authority) the fish could be delivered to private processors on schedules and at prices agreed to in written contracts. This option is not under current discussion, because, like the full private property option, it would entail massive alterations of existing legal and institutional arrangements for fishing.[5]

In comparison to full public or private ownership of fish stocks, the two common limited access options represent moderate alterations in the current system of open access.

## Elements Of A Limited Access System

It is useful to organize a discussion of license limitation and individual quotas around a list of essential program elements. The following list was recently developed for a discussion of limited access to Pacific coast groundfish.[6]

1. Scope of fishing activities covered,
2. Means of limiting access,
3. Basis for initial allocation of harvest rights,
4. Transferability of harvest rights,
5. Duration of harvest right,
6. Means of altering number of licenses or quotas,
7. Means of settling disputes regarding issuance and transfer of rights.

Options available for each of these are described below.

### 1. Scope of Fishing Activities—Gear, Species, Areas

Fishing rights under limited access could be very broad (e.g., any groundfish in the Gulf of Alaska using any gear during any season), or they could be restricted to specific species and gears (e.g., halibut and sablefish caught by longline in the Kodiak area). Licenses or individual fishing quotas can be subject to limitations on quantity of gear, timing, fish size, and/or incidental catches.

These additional restrictions may incorporate many of the conventional fishing regulations already adopted in the fishery management plans.

**Fishing Gear**—Gear types currently used to harvest groundfish are fish pots, bottom and midwater trawls, longlines, and other hook and lines. A license system could include all gear types under a single license, or there could be separate and specific licenses for different gears. An individual fisherman quota system may also designate specific authorized gear types. But it is not necessary for individual quotas to be limited in this way. New Zealand's ITQ system, for example, permits the quota owners to choose among gear types.

Existing regulations prohibit the use of drift or set gill nets, beach seines, or other gear for groundfish. Continuation of this gear limitation would prevent the addition of gears that are not now important. Current Gulf of Alaska regulations preclude the use of pot gear to catch sablefish in the Eastern Area, and they will expand this prohibition to the entire Gulf in 1989. It is simple to incorporate this planned phase-out of pot gear in either license limitation or individual quota systems. Licenses specifying pot gear would specifically denote the prohibition of pots after 1989 in the Gulf of Alaska; and individual quotas for sablefish would stipulate that fish pots were unacceptable after the same date.

**Species**—Alternatives include at least the following three: (1) All groundfish species included under a single limitation system; (2) Separate licenses for various species or groups of species; (3) Some species included while others remain open access. For example, licenses for fixed gear only (longline and fish traps) could be established for harvest of halibut, sablefish, rockfish, and Pacific cod. Licenses for trawl gear would be intended for harvest of various flatfishes (excluding Pacific halibut), pollock, sablefish, Pacific ocean perch, other rockfish, thornyheads, Atka mackerel, squid, and Pacific cod.

**Geographical Area**—Licenses and individual quotas may pertain to the entire EEZ, or to more limited fishing areas. Allocation of quotas to specific areas and gear types assures some geographic spreading of fishing mortality that may be necessary for stock conservation when substantial excess fishing capacity threatens to overfish sub-stocks. A drawback to extensive geographic subdivision, is that it may cause inefficiently small scale fishing operations, and, by reducing the fisherman's flexibility, subject fishermen to more income uncertainty than under existing regulations. Thus a trade-off between precision in control of area specific harvests and flexibility of fishing operation must be evaluated.

An alternative approach is the staggered openings and closings as used in the halibut fishery. Since most groundfish species have not yet attracted a vast excess of fishing capacity, it should be unnecessary to attempt a fine geographic distribution of effort through restrictions on licenses. Only divisions based upon established scientific assessments of species and sub-stock populations structure would be necessary.

Jurisdictional scope must be considered. Federal authority could limit licenses for fishing in EEZ areas, leaving state waters open. A combination State and Federal license, or at least a coordinated overall effort, could be helpful in preventing the territorial sea fishery from eventually becoming a troublesome unlimited sector.

### 2. Means of Limiting Access

Whether the license limitation or individual quota option is selected, there are still a number of choices regarding how the fishing rights should be assigned to entities. A license or individual quota can be attached to the vessel (as in the California salmon license program), or it can be assigned to an individual (as in the Alaska salmon limited entry system), or it can be held independently of vessel ownership or personal fishing activity (as in the New Zealand ITQ system). Yet another option would be to assign quantitative rights to large, integrated firms involved in processing and fishing vessel operation (as in the enterprise quotas of Atlantic Canada).

Additional limitations are often placed upon who or what is licensed. For example, corporations are not permitted to own Alaska salmon licenses. Conditions for leasing fishing rights, or required presence of rights holders aboard fishing vessels can be controlled through ancillary restrictions. A prohibition on corporate ownership would be troublesome in groundfish, since the large capital investments involved can rarely be mounted by individual persons, and the limited liability of a corporate entity is a major factor in attracting investment through capital markets. Other restrictions on ownership may, however, accommodate national policy objectives associated with Americanization of the fishery. Examples include: (1) stipulation that only U.S. citizens own harvest rights, (2) limitation to citizens or corporations whose owners are U.S. citizens, and (3) requirement that licensed fish be harvested by vessels constructed or re-fitted in U.S. shipyards.

### 3. Basis for Initial Allocation

An equitable basis for starting a limited access program is perhaps the most critical requirement. Once the system is well established, the initial allocation will be of diminishing importance. But, a license system begun badly, through a highly contentious allocation phase, is likely to develop political opposition which can lead to repeated re-opening and judicial review of the allocation decisions. Such reviewing constitutes a threat to existing license or quota holders, and it can undermine confidence in the system. Long term planning and rational investment decisions depend upon the establishment of secure and stable access rights. Such stability depends upon broad public acceptance of the system. Hence, a decisive, legally defensible, and equitable initial allocation is critically important.

As noted in Section III above, several different concepts of equity are in common use. If equity is taken to mean equality of fishing rights (as with inalienable rights like free speech, voting rights, etc), then every citizen should have the same right to fish. This concept of equity is consistent only with the open access system. Limiting access clearly implies the rejection of equality as a basis for equity. A variant on equality of fishing rights is equality of opportunity to obtain fishing rights. A practical approach to achieving equality of opportunity, without allowing everyone to fish, would be to issue fishing licenses by lottery. A lottery would be equitable in providing everyone an equal chance to fish, even though only a limited number of winners would obtain the fishing rights and associated benefits. Neither equal rights nor equal opportunity to obtain rights are commonly adopted as criteria for initial allocations in limited access systems.

In previous resource allocation systems past sacrifice and established use are common criteria for allocation. Elizabeth Rolph (1983) reports that governments allocating property rights to resources previously used communally nearly always use past use as a criterion. Agency decision-makers apparently seek to avoid a direct redistribution of economic wealth. While any modification of resource use rights will inevitably cause some alteration in distribution of economic benefits among users and ancillary industries, accommodation of historic use in allocations of rights will tend to avoid abrupt redistribution of wealth. Allocation of resource use rights based upon past use and financial commitment is a specific case of the "no losers" approach. Thus common administrative practice and economic theory support historic use as an important criterion for assuring equity in allocating fishing rights.

Application of the "no losers" criterion to groundfish limited access would be feasible, at least as applied to identifiable groups of fishermen. All existing gear types, regional groupings, and individuals with documented fish landings could be protected from "losing" in the initial allocation of fishing rights by assigning to them a right to harvest at least as much fish as they had been harvesting in the past.

Past participation in the groundfish fishery as a basis for initial allocation would qualify thousands of longliners, pot fishermen, coastal trawlers, joint venture trawlers, and factory trawlers. Also, extension of the criterion to include those with recent substantial investment in construction or conversion of a vessel for entry into the groundfish fishery before a cut-off date would add a number of additional qualifiers. Another consideration for qualification could be participation in related fisheries such as the Washington-Oregon-California groundfish fishery, the king or tanner crab fisheries, the Gulf of Alaska or west coast pink shrimp trawl fisheries. Inclusion of these could add at least another five hundred fishing vessels or two thousand fishermen.

In sum, a license limitation system allocating fishing privileges to everyone with a history of participation in groundfish or related fisheries, would begin with excessive fleet capacity. To effectively limit fishing capacity, the entry criteria must be tightened up; or the fleet could be reduced later (e.g., through a license buy-back program), or the licenses must be encumbered by significant ancillary restrictions (such as on vessel size, gear, or area fished). Clearly, the initial allocation scheme determines the necessity for other program elements such as fleet reduction and restrictions on licensed fishing rights.

The Alaska salmon license program reduced the number of initial permits issued by establishing eligibility rules based upon past participation and economic dependency. A point system was developed to rank applicants, giving most points to those who would experience the greatest hardship if excluded from fishing. A fixed number of permits were issued to applicants in order of points. The assignment of points had to be based upon specific facts that were not always clearly documented. Consequently, various disputes and legal challenges to permit application decisions became a significant source of controversy and expense for the Alaska Commercial Fisheries Entry Commission. In comparison to wholesale inclusion of all past participants, the Alaska salmon permit allocation process was complex and expensive (Schelle and Muse, 1986).

Initial allocations of individual quotas or shares would also need to meet equity standards. The initial shares could be based upon past harvests, future planned harvest, or some explicit formula including past harvests and quantitative measures of investment or vessel capacity. Total allocations of quotas to domestic fishermen could be kept to not more than the total allowable catches. Where the fishery has not yet utilized the full potential annual yield, additional individual quotas could be distributed after the initial allocation through direct sales, auctions, lotteries, first come-first served, or other methods not based upon historic use.

### 4. Transferability

Whether licenses should be transferable by sale, gift, and bequest used to fuel a lively debate. The issue now seems to be decisively settled in favor of transferability. To be able to sell a fishing license or quota share provides a means to convert value of prospective future earnings into cash. The prospect of a potential future sale makes license holder more attentive to resource conservation needs, and transferable fishing rights provide valuable business collateral and become a source of income in retirement. Owning a license in a limited fishery is a bit like owning a share of the fish stock, although it may be worthless if fishing capacity is not effectively controlled.

Arguments against transferability include the notion that fishing rights should not have monetary values placed on them, that the market value placed on freely distributed fishing rights represents an unfair windfall gain to the original recipients, and that market prices for licenses represent a significant barrier to new entrants. The first argument stems from an ethical judgement that is irreconcilable with private markets in property rights (i.e., in opposition to capitalist economic conventions). If such ethical standards were widespread, it would indeed be futile to discuss marketable fishing rights.

The second argument holds that it is unfair to distribute economic wealth based upon criteria used to allocate fishing rights. It is true that license ownership patterns influence the distribution of wealth derived from fishing. If licenses are awarded free of charge, the initial license holders are given a potentially valuable capital asset. The value of this capital asset (based upon profitability of fishing) will be reflected in a market price. While it would be difficult to claim that any awarding of capital assets is unfair, the particular pattern of capital assets associated a limited access system could be unfair. If the initial allocation is done fairly, then indeed the asset values will have been fairly distributed.

The third argument against market transfer involves some confusion regarding the role of capital asset values in the economy. A successful license or individual quota program that stabilizes fishing profits at a higher level, should foster rising license or quota prices. Sellers may make significant capital gains, and new entrants to the industry will face larger start-up capital costs than those faced by the original group of licensees. The additional cost of entry will not be a barrier to entry, however, since the value of the license reflects the greater earnings potential, and financial institutions are more likely to lend the necessary start-up capital to a new business that has an established share in a more stable industry.

### 5. Duration of Fishing Rights

Like transferability, the question of duration is generally settled, with permanent rights being the preferred option. Annually renewable licenses are still used in some fisheries (California having most of the existing license systems of this sort), and limited duration, 10-year, licenses were recommended by the Pearse Commission (Pearse, 1982). Limited duration, however, has two distinct disadvantages. As the license nears its termination date the permit owner will suffer all the disadvantages of a non-transferable permit, and the short-timer will have reduced incentive to conserve fish stocks. It is recommended that harvest rights, whether licenses to fish or individual quotas, be perpetual.

### 6. Means of Adjusting Number of Licenses or Quotas

Since the initial number of licenses or initial allocation of individual quotas may not be the optimal number, managers will need a mechanism for adjustment. Both the economic efficiency and management flexibility objectives require this. With license limitation, if the initial number is too large, reductions in numbers of outstanding licenses through "buy-back" or attrition will be desirable. A buy-back fund may be created from royalties on fish landings, or it may be taken from general tax revenues. In the first case, both the remaining fishermen and those selling licenses to the buy-back authority will benefit; and it will not impose any additional cost on taxpayers. In the second case, all fishermen potentially benefit, but the taxpayers may not. Without a buy-back program, and assuming licenses are non-transferable, the fleet could be reduced through attrition of bankrupt, injured, or retired fishermen. This approach may ultimately decrease excess capacity, increasing average profits for remaining fishermen, but it imposes a hardship on those leaving the fishery.

If an increase in numbers is warranted, new licenses may be issued by auction, lottery, or selection from a list of qualified applicants. The latter selection can be based upon first-come, first-served, or applicants can be selected by a complicated point system. These same mechanisms can be used in any subsequent allocation of additional licenses.

With individual quotas the initial allocations will probably not exceed total allowable catches. Adjustments to outstanding quotas will be necessary, nevertheless, in order to tailor annual catches to fluctuating fish stocks. The available procedures will depend upon whether the individual quotas are absolute quantities or shares. Since quota shares are percentages of total allowable catch, adjustment of annual total outstanding quota rights requires only that advance notice be given to quota holders. With fixed quantity individual quotas, the management agency will need a procedure to issue additional quotas for fish species that are in high abundance and to reduce outstanding quotas for fish species that are in reduced abundance. This procedure can include purchase and sale of quotas by the management agency. The New Zealand groundfish system seems to be the only case of market operations to adjust quotas.

### 7. Means of Settling Disputes

Under any system of private fishing rights, disputes will arise regarding initial qualifications of individuals to participate in the fishery, and concerning subsequent transfers and usage of permits or quotas. During the initial allocation of licenses or individual quotas, documentation of facts will be an important element of the process, especially facts concerning past groundfish harvests, commitments to invest, and any other elements adopted as allocation criteria. There are several possible approaches to handling these. Any of several different authorities could settle disputes: (1) a special review board appointed by the NPFMC or NMFS; (2) a Federal official like the NMFS Regional Director or NOAA Administrator; or (3) an Administrative Law Judge could be given jurisdiction. It is important to establish the procedures well before any complaints are lodged against the system.

During the subsequent operation of a limited access system additional disputes are bound to involve questions of ownership and delegated authority. With transferable licenses and quotas, it will be necessary to establish exactly when ownership changes hands. However, since transactions in fishing rights will differ little from other commercial transactions, existing judicial procedures should be capable of handling associated disputes. A specific statement in the limited access program documentation should clarify the intended role of civil courts and note any special procedures, such as registration of licenses and individual quotas, needed to clarify ownership of fishing rights.

## Relationship to Conventional Regulations

Recent studies have uniformly concluded that license limitation does not obviate the need for conventional regulations limiting fishing mortality rates on a stock by stock basis.[7] Because groundfish fishing operations often range over several species and areas, limiting the total number of vessels will not restrict fishing effort for species needing stronger protection due to diminished abundance or for high-priced species that are more avidly pursued. Hence, annual harvest quotas, closed seasons, area closures, and other direct regulations will be needed despite license limitation.

Individual quotas more directly limit fishing mortality rates for individual species, but there will remain a need to control the pattern of fishing to obtain optimal results. Allocations among gear types, size limits, prohibited species quotas, and closures of some areas to trawl gear could be retained even under a individual transferable quota system. It is unrealistic to assume that conventional regulations will be entirely, or even substantially, dismantled, but it is reasonable to suppose that limited access, especially the individual quota option, will permit significant simplification and reduction in the number of these regulations.

## Making Limited Access Consistent with National Fishery Policy

Creation of marketable fishing rights creates a new instrument for ownership and control of fish production. Free trade in these rights will clearly open the door to foreign ownership of fishing rights, just as it is now open to foreign investors in other assets. Substantial foreign participation is already a fact of life in the U.S. groundfish fishery, with foreign companies having direct and equity investments and as well as other financial ties to many of U.S. fishing companies. Some industry spokesmen note that the groundfish fishery is being internationalized, not Americanized.

Clear standards for foreign ownership of fishing rights can reconcile limited access with the national fishery policy. Two distinct options are apparent: (1) We could permit fishing rights to be traded without regard to nationality, or (2) we could establish requirements for American ownership. The first option is equivalent to the policy established for almost all U.S. assets, such as real estate and farm land. Fishing licenses and individual quotas, represented by official certificates and records, would be purchased and sold by foreign and domestic individuals and business firms with no unusual restrictions. The second option would require careful development of specific ownership requirements that limit foreign participation in fishing rights.

Free trade in fishing rights would permit foreign fishing companies to control the U.S. catch in few ways that are not now possible. Assuming that the MFCMA is not amended, and that preference to domestic fishing and processing firms in quota allocations is retained, allocations would continue to be made first to U.S. processors, then to joint venture companies, and then to direct foreign fishing. Foreign participation in ownership of U.S. fishing companies does not make the company a foreigner for allocation purposes now, and this would presumably not change under limited access. It is unclear, therefore, that foreign ownership of individual fishing quotas or licenses would permit foreign firms to gain greater influence over the allocation process, with negative consequences for American participants.

However, if it is decided that foreign ownership should be limited, we need to develop detailed criteria on levels of permissible foreign participation, taking full recognition of the complexity of ownership arrangements. For example, New Zealand prohibits direct foreign purchase of quotas, and imposes a limit of 25 percent foreign ownership in companies that own quotas. In the U.S. a ban on foreign ownership of quotas could be implemented by allowing only U.S. registered vessels to catch fish using licenses or quotas. This would relegate the problem of defining U.S. ownership to the maritime registration procedures.

An effective restriction on foreign ownership of companies owning quotas must be much more complicated than this, of course, since "foreign ownership" needs to be defined very clearly. Most large fishing companies are corporations. Some of these are publicly held, in which case ownership is a matter of record, and some are privately held. It is not unusual for a fishing corporation to be wholly owned by another corporation, nor for one corporation to own shares in another corporation. To trace the lines of ownership for marketable fishing licenses and transferable quotas would require the employment of corporate legal specialists, unless, of course, some strong restrictions on forms of fishing business organization are implemented. It is beyond the scope of this study to develop the necessary rules and standards for limited foreign ownership.

## Conclusions

This review of limited access options supports a variety of conclusions that do not differ greatly from those reached in previous studies. Under ideal circumstances, limiting access directly addresses the objective of improving economic benefits by bringing fishing capacity in line with total allowable catches. Limited access also may enhance fish stock conservation by helping to spread fishing effort over seasons and substocks, and by decreasing the prevalence of discards during short fishing seasons. Because replacement of open access with limited access changes the structure of the commercial fishing business, equity in the distribution harvest rights is the paramount concern in the initial allocation of limited licenses or quotas. Enunciating explicit standards of equity is a most difficult task for management agencies and represents a potential roadblock to establishment of limited access.

The objective of maintaining flexibility in management calls for procedures to vary total allowable catches and continued use of ancillary regulations such as area closures, gear restrictions, fish size limits, and some prohibited species designations. Flexibility in commercial fishing can be dealt with by providing transferability of licenses or quotas, by creating relatively wide geographic scope for harvest rights, and by minimizing gear restrictions. Recognition of national interests in continued Americanization of the groundfish fishery may require specific restrictions on foreign ownership of licenses, on registration of vessels harvesting individual quotas, and on foreign participation in companies owning fishing licenses or quotas.

Of the two versions of limited access considered, individual quotas most clearly facilitates achievement of economic objectives. Assuming that the initial allocation of individual quotas is consistent with the total allowable catches, managers need not close fishing seasons to conserve stocks, and fishing companies can maximize their profits from harvest by choosing appropriate timing, and location of fishing. License limitation cannot effectively limit fishing capacity unless either (1) the number of licenses initially issued is severely limited, or (2) a license buy-back program is funded and successfully carried out, or (3) significant additional gear or vessel restrictions are attached to the licenses. Even with these measures, license limitation is a second best form of harvest capacity control simply because fishing capacity of a given fishing vessel can be expanded through investment in technical improvements.

With either license limitation or individual quotas, the most critical management decisions are choice of initial allocations and choice of restrictions on ownership of harvest rights. Because initial allocations strongly influence the ultimate distribution of costs and benefits from the fishery, the equity issue is the paramount concern in initial allocation. Rights based on historic use and/or current commitment to the fishery could meet a standard of equity based upon of creating "no losers" of harvest rights. Second, the assignment of fishing rights to individual fishermen, to vessel owners, to vessel operators, or to persons regardless of ownership or participation in the fishery, will determine initial bargaining strengths of competing commercial interests. Most existing license and quota systems assign the rights initially to owners of fishing vessels.

Further development of limited access in Alaska groundfish will have to address a series of specific issues including: whether to license fishing or processing; whether to explicitly allocate among joint venture, factory trawler, and coastal trawler fleet; whether to include longline and trawl fleets in a single system; and whether to preserve an open access portion of the fishery to preserve intangible benefits associated with a "way of life" rather than conventional economic returns.

The deepest and most contentious issues are likely to represent the most difficult hurdles to establishing a limited access system. Because transferable quotas and licenses permit exchange among people of different regions, a transferable fishing rights program implies acceptance of market competition as a regulator of the location and structure of the fishing industry. Whether specific coastal communities or high seas fishing fleets eventually predominate in the fishery will not be under the control of fishery managers once the market system is established. Political favors for special interests will be difficult to deliver, diminishing the power and influence of management agencies. Thus, limited access, especially the individual tradeable quota system, can overturn long-standing relationships among government agencies, political actors, and industry participants. This fact, and the uncertainties regarding distribution of initial shares, probably accounts for the current high degree of suspicion and opposition to limited access.

## Endnotes to Section V

1. License limitation has been extensively reviewed and analyzed in Rettig and Ginter (1978), Sturgess and Meany (1979), Pierce (1982), Rettig (1984), Anderson (1985), Mollett, ed. (1986), and Huppert, ed. (1987).

2. Landings taxes, fees, and royalties are sometimes included in the list of access limitation methods. While taxes and fees can create proper economic disincentives to overfishing, I do not include them, because they do not involve an act of limiting access to the fish stock to any particular group of people. With the kinds of limited access considered in this paper, a landings royalty or tax could be used to redistribute the economic returns from fishing, but would not be an instrument of limitation.

3. The original British Columbia salmon license program, for example, created permanent "A" licenses that permit replacement of vessels, and limited term "B" licenses which were to phase out in 10 years and remained attached to the original vessel. See A. Fraser (1978).

4. Japanese Fisheries Cooperative Associations exercise sea-tenure rights that are equivalent in many ways to land tenure rights. It is clear from the study of the Japanese system of coastal fishing rights, that their establishment stemmed from a long tradition extending back to the feudal period. See K. Ruddle (1987).

5. Dr. E.A. Keen, San Diego State University, is one proponent of this public enterprise approach. Detractors of the approach would point out that public enterprises tend to be inefficient and unresponsive to diverse public interests. It is unclear from general principals whether these sources of inefficiency would be greater or smaller than those inherent in private use of common property marine fisheries.

6. See Huppert, 1987; p. 13-17.

7. See in particular R. L. Stokes (1983), and S. Hanna and W. Silverthorne (1987).

## VI. Implementing Improved Groundfish Management

The rapid expansion in domestic groundfish harvesting and processing alters the economic and political circumstances confronting the management system. Americanization of the fishery (1) shifts the focus of conservation measures from foreign to domestic fishing, (2) creates an opportunity for gaining greater economic returns from the fishery resources, (3) increases the need for meticulous information collection from the domestic fishery, and (4) initiates extensive shifts in patterns of economic activity. Besides changing the task of fishery managers, new rivalries are kindled, and existing conflicts among competing segments of the industry are renewed. The ongoing economic transformation of the fishery will undoubtedly materialize in additional, yet unanticipated, ways. Devising an equitable treatment of competing user groups will be a critical task for improving fishery management.

This report has explored several aspects to improved groundfish management, covering both modified conventional regulations and various forms of limited access. Sections II through V have delineated management objectives, summarized emerging problems, characterized new options, and highlighted controversial issues. This concluding section draws together the various logical threads of the foregoing discussion, reviewing earlier observations and conclusions, and suggesting specific management approaches to achieve the major objectives. The presentation is focussed on a two illustrative proposals to meet the various management needs and objectives.

The review of conventional regulations in Section IV revealed no new and startling opportunities, but it did confirm the importance of imposing total allowable catches, sub-dividing quotas to geographic areas based upon population structure, and applying fish size and gear regulations to increase yield and harvest values. Some modifications, such as allocation of incidental catch of prohibited species among target and non-target fisheries, can increase the landings and economic value of halibut, for example. Just as importantly, reallocating halibut as incidental catch in non-halibut longlining will help facilitate the economic harvest of alternative target species such as Pacific cod. Beyond these specific suggestions, no substantial improvements in the basic set of conventional regulations have been identified.

While this report was being written, the North Pacific Fishery Management Council voted to develop a limited entry system for the longline sablefish fishery, and it adopted provisional cut-off dates for determining qualification for entry into the groundfish fishery. The Council appointed a Future of Groundfish Management Committee to consider and recommend directions for improving management of the fishery. It is not yet clear whether the Council will decide to limit access to Alaska groundfish, and, if so, what specific objectives will be embraced. Whatever course is taken by the Council, however, successful implementation depends upon a clear, logical plan linking policy objectives, choice of alternatives, and program elements. The Council's thwarted attempt at license limitation in the Pacific halibut fishery demonstrated the vulnerability of an incomplete limited access plan.[1] An initial moratorium or license limitation for groundfish, for example, is unlikely to be easily sold as a useful step toward economic rationalization unless it is teamed with a more comprehensive, long run approach to management.

A comprehensive plan will need to promise real economic gains through effective control of fishing effort. It will need to meet standards of fairness and equity in the allocation of harvest rights and in the resulting distribution of economic rewards; including measures to avoid undue concentration of harvest rights, and provisions for sharing resource rents with the public "owners" of the fish stocks. It will need to allow flexibility in providing for both fish stock conservation and normal commercial business planning. Finally, a comprehensive limited access plan will need an enforcement, monitoring, and fishery data collection plan meeting the minimal requirements of scientists and enforcement agents.

Meeting all these criteria will require careful planning, review, and technical scrutiny. To assist in that task, this concluding section organizes the ideas expressed earlier by developing strategies for limiting access. These strategies are not formal proposals and they do not seek to preempt other proposed groundfish management systems. Rather, they illustrate promising strategies for change. These illustrative proposals are intended to draw criticism and to foster additional discussion of management alternatives.

## Strategies for Future Management of the Groundfish Fishery

Each of the two alternative strategies developed below includes a limited access management system. The first alternative proposes an initial license limitation system, followed by individual transferable quotas. The second strategy starts directly with individual quotas and follows more closely the intent of the Americanization policy. The two approaches are designed to appeal to different interest groups.

### STRATEGY 1

The strategy is developed in four steps: (1) A groundfish license limitation program establishes the numbers of harvesters and specific conditions on transfer among license owners; (2) an expanded enforcement and monitoring program including at-sea observers, audits of landings receipts, Coast Guard sea and air operations, and scientific sampling of catches; (3) allocation of transferrable share quotas to groundfish license holders; and (4) a funding mechanism for management functions that could involve various alternatives to Federal general funds, including annual license fees, royalties on quota shares, and charges for at-sea observers.

The strategy could be implemented in the sequence presented, or some steps could be combined and implemented simultaneously. Truly comprehensive and rational planning might call for the whole strategy to be refined and implemented at once. Experience indicates, however, that key participants in the process will not be ready to deal with the later steps, such as new funding methods, until the benefits of earlier steps are realized.

**STEP 1: LICENSE LIMITATION.** A groundfish license would be issued to owners of all U.S. registered vessels harvesting groundfish in the EEZ in the Gulf of Alaska, Bering Sea, or off the Aleutian Islands during a base period, possibly 1985 through 1987. Each license would name one vessel authorized to fish groundfish. Licensees would include factory trawlers, coastal trawlers, joint venture trawlers, longliners, and other vessels using legal gear to land pollock, cod, sablefish, soles, flounders, Atka mackerel, rockfish, or other groundfish. Floating processors, motherships (of U.S. or foreign flag), tenders, and cargo vessels would not receive licenses, although they would continue to obtain the permits required under the existing groundfish regulations.

Operational rules required to monitor and enforce the license limitation program include the usual possession and display requirements. Any vessel owner intending to harvest groundfish, or to deploy any gear normally targeting on groundfish species must possess a groundfish license. Penalties and fines for fishing without a license would have to be established at a level sufficient to deter cheating.

Each vessel licensed would be assigned to one of the following classes: hook and line or pot fishing vessel, trawl vessel delivering to shoreside or at-sea processor, factory trawler of less than 200 feet in length, factory trawler of 200 to 300 feet in length, and factory trawler of greater than 300 feet in length. Designation of class of vessel would be based upon registration records and legal documentation of fish landings during the base period. Vessels with records showing more than one class (e.g., a vessel using both longline and trawl) would have a special license naming both gear types.

Owners of vessels not fishing during the base period for one of the following reasons would have a right to apply for a new license within twelve months: (1) vessel was fishing in a different fishery (e.g., tanner crab) or elsewhere (e.g., Pacific coast) but had a history of fishing groundfish off Alaska, (2) vessel was laid up for repairs, or conversion during the entire base period, (3) vessel was not yet operational during the base period but was in construction for entry to Alaska groundfish fishery. The standards for issuing licenses to vessel owners not qualifying on the basis of landings would be formulated by the NPFMC, and would include a definition of what constitutes adequate evidence.

The groundfish licenses would be transferable by private transaction among vessels within classes, allowing new vessels to enter the fishery as another vessel exits. License transfers would be registered with the NMFS Regional Offices within one week.

In addition to registering vessels, buyers of groundfish would need to be licensed so that records can be kept of all sales and purchases. Foreign and domestic buyers would be required to maintain and periodically submit records of quantity, condition, and species of fish bought. This information would be equivalent to existing State requirements for "fish tickets."

DISCUSSION OF STEP 1. Because it allows license transfers within vessel classes, this first step is not a simple moratorium. It limits the size of the domestic fleet but permits some substitution of vessels. Because vessels could be upgraded within class, total fishing capacity would not be effectively limited by this license limitation program. It is intended to be a temporary and transitional step to an individual quota system. It would be inappropriate as a permanent system, because the flexibility among vessel classes and growth in the factory trawler fleet is not sufficiently accommodated.

**STEP 2: UPGRADED MONITORING AND ENFORCEMENT.** After the licenses are established, the system for monitoring and enforcement of groundfish catch quotas, prohibited species regulations, and other conventional regulations would be reviewed and upgraded as necessary. Scientific sampling requirements and on board observer coverage necessary for monitoring total catch, landings, and usage in at-sea processing plants would be established by joint committees of industry, NPFMC, and management agencies. A full plan for Coast Guard surveillance of foreign and domestic vessels at sea, state/Federal agency audits of catch records, radio and logbook reporting requirements, and on board observer protocols would be designed with the objective of providing accurate and complete information regarding withdrawals of groundfish by U.S. vessels in the EEZ. NMFS and/or the NPFMC would publish a complete and detailed document for review and adoption.

DISCUSSION OF STEP 2. The intention here is clearly to provide adequate data for enforcement, monitoring, and scientific assessment of groundfish catches. Under this strategy, the data system would be developed before the at-sea processing fleet grows substantially beyond its current size. This is, and will continue to be, a significant source of controversy. Shoreside processing companies and many management agency biologists may contend that observer coverage of domestic trawlers should be the same as coverage of foreign vessels. Some operators of domestic factory trawlers will oppose mandatory observers as an unreasonable and costly intrusion. Because there are such strong economic incentives to under-report fish caught and processed at sea, however, unmonitored operations could destroy the credibility of a conservation regime. An individual quota system that does not impose some mandatory coverage of at-sea operations would be particularly vulnerable. Thorough coverage of on-shore landings may require observers in shoreside processing plants to a similar degree. While it is not the purpose here to provide a detailed design for the data system, I emphasize the importance of rigorous data collection process to any management system that relies on either aggregate or individual quotas.

**STEP 3: ISSUE SHARE QUOTAS TO LICENSED OPERATORS.** Once the catch monitoring system is sufficiently upgraded to assure completeness and accuracy of species catch reports, the licensees would be issued shares of the total allowable catches. Documentation would be assembled regarding each vessel's catch of groundfish during the previous five years. A formula for determining shares would be developed for making an initial allocation. This formula could have some of the following features:

1. Each licensee could choose the year of record for use in establishing his or her share;
2. Licensees not having an adequate catch record could choose to take a share equal to the class median. For example, a longliner having fished only a partial season due to mechanical breakdowns could opt for a share equal to the median catch by longliners of similar length.
3. Allocations of shares would be expressed as a percent of the current year's total allowable catch. The percent allocated to a licensee would be computed by dividing that licensee's catch of record by the Allowable Biological Catch in the year of record. If the sum of the shares calculated by this procedure exceeds 100 percent, then each share will be reduced proportionately until total of the shares issued equals 100 percent.
4. For some species the shares allocated will total less than 100 percent of the TAC (e.g., for species like Pacific cod that are not fully utilized). Additional shares for the under-utilized species would be issued on a first-come, first-served basis to original licensees or to any new owners of groundfish vessels. The size of these new shares would be based upon the typical share already allocated to license holders. To avoid non-productive speculative activity, new shares would be non-transferable for one year, and would be cancelled if the owner does not harvest a substantial portion of the share allocated within a year.

Allowable catch for any foreign fishing still occurring, would be limited to the Total Allowable Catch minus the sum of joint venture and fully domestic quotas. No shares would be issued for foreign fishing.

Individual quotas would be transferable among groundfish license holders and to new vessel owners who have appropriately registered with the NMFS Regional Office. A computer-linked trading system would be established in all major fishing ports, having a continuously updated list of quota share holders and their share holdings. Actual catch data would not be publicly available during the fishing year in accordance with data confidentiality requirements. All transactions among license holders are required to be recorded expeditiously to the NMFS Regional Office (e.g., within one week of sale).

Once the quota trading system is operational, the number of groundfish licenses would no longer be limited, but each participant would continue to be required to register with the NMFS Regional Office. This would permit screening of quota ownership for excessive accumulation of shares and for foreign participants. To prevent excessive control of shares in the groundfish fishery, no single entity would be permitted to own a preponderance of the total quotas in either the Bering Sea and Aleutian Islands area or in the Gulf of Alaska.

The Americanization policy could be preserved with a slight modification to this strategy. The species quotas would be sub-divided into fully domestic and joint venture, with the JV share equal to TAC minus domestic. To encourage the phase-out of joint venture fishing, the joint venture vessel's initial quota shares would be calculated as a percentage of the overall joint venture allocation rather than of the TAC. Thus, as the domestic fishery expands and takes larger shares of TAC, the joint venture shares become smaller and smaller as the pool of JV allocation diminishes. To obtain domestic shares, vessels active in the JV fishery would apply for shares of species that are not already completely claimed for DAP fishing. Once obtained they would deliver these harvest shares to U.S. processing plants or to U.S. registered at-sea processors.

DISCUSSION OF STEP 3. These quotas would be percentage shares of the annual TAC, so that actual quantities for a given share will fluctuate with the annual TACs. This is somewhat less convenient than ITQ quantity shares for the vessel owner, but it is vastly simpler for the management agencies to alter TACs if they do not have to buy and sell quotas in the open market.

Another important feature of this individual quota plan is the free distribution of initial shares based upon historic use, combined with distribution of additional share quotas for under-utilized species. To retain their shares, share owners would have to remain active in the fishery. This would prohibit the stockpiling of unused quota shares.

An important issue not explicitly dealt with in the individual quota description was the method to determine whether a fishing vessel is a U.S. operation. Current Americanization policy gives higher priority to fully domestic fishing than to joint venture fishing in the allocation of TACs. With tradeable quotas, the ownership of shares will change frequently, and the nationality of the ultimate owners will not be immediately apparent. The requirement that each quota owner maintain registration with the NMFS Regional Office provides a possible mechanism for reviewing ownership, but developing specific procedures for determining nationality of owners may require substantial legal expertise.

STEP 4: ESTABLISH A SYSTEM OF SHARED FUNDING. The costs of collecting and analyzing information for stock assessments and annual TAC determinations, as well as costs of routine monitoring and enforcement of quotas, should be shared equitably between the general taxpayer and private businesses operating in the groundfish industry.[2] Two key issues will need to be resolved in establishing a shared funding system. First, appropriate principles for dividing costs between taxpayers and commercial firms needs to be established; and, second, a mechanism needs to be designed for collecting funds and appropriating them to research, monitoring, and enforcement tasks.

The first issue could be dealt with pragmatically by establishing agreement on one of the following principles:

1. As the groundfish processing fleet becomes fully domestic, the share of management costs paid directly by the U.S. taxpayers should not increase. Because the foreign processing fleet paid for the costs of running the foreign observer program, the expansion of the domestic processing fleet with similar observer coverage would, without a mechanism for industry contributions, require increasing support from public funds. One approach to fairly distributing the burden of cost would be to create a funding mechanism relying on contributions from the industry.
2. Extensive resource surveys, stock assessments, and management institutions (NPFMC) involve large fixed costs that accompany resource management responsibility, whereas the additional cost of monitoring and enforcing regulations on an additional vessel as it enters the fishery is directly attributable to the investment or operating decision of a commercial firm. The former expense is logically a public responsibility, while the latter cost should be levied on the commercial firm. This logic is consistent with an incremental, "user pays" approach to resource management.

Acceptance of either of these lines of reasoning would support the collection of an amount of money directly linked to the costs of monitoring and enforcing management rules on groundfish vessels. Several sorts of fees could be considered: a lump-sum license fee, an *ad valorem* quota share royalty, or a landings tax. The license fee is easiest to administer, as it involves simply collecting an annual amount from each licensed groundfish vessel owner. The *ad valorem* royalty would be calculated, like a property tax, as a percent of the value of groundfish shares held. The value of the fish could be based upon recorded quota share sales. Because the shares change hands regularly, the tax would be based upon registered shares held as of some particular date, possibly January 1.

The third option, a landings tax, is the most complicated to administer because it requires either (1) the tax be collected after each and every transaction (many of which may occur at sea), or (2) that a cumulative tax payment be collected periodically based upon cumulative groundfish landings values. The annual royalty on shares held is preferable to the tax on catch, because it is administratively simpler and because it creates far less incentive to distort catch records and sales receipts.

Whatever basis for calculating specific charges for fishing vessels is accepted, the funds collected would be placed in an ear-marked fund for sole use of the groundfish monitoring and enforcement program. If implemented by the Federal government, tying the collection of funds to a specific use would require special authorization of the Office of management and Budget, and possibly legislative action. As noted earlier, the MFCMA does not now provide a mechanism for collecting substantial fees for fishing to cover management costs. Consequently, further exploration of industry funding of research and management activities will have to proceed through voluntary organizations or through legislative action.

DISCUSSION OF STEP 4. This step is likely to provoke substantial opposition from those paying the fees and lukewarm support from those not paying the fees. Consequently, this is a politically difficult step to take. It is justified on equity grounds, however, as a reasonable contribution by those standing to gain the substantial economic benefits that the individual quota system can provide. Whether funding from the commercial industry should cover just the costs of catch monitoring, or whether it should shoulder a greater share of the stock assessment and management costs is a contentious issue. The proposed solution to this follows the spirit of the "no losers" standard; neither the taxpaying public nor the commercial fishing interests obtaining share quotas will lose.

Specific proposals for fees should be designed to meet specific management costs. Since this study did not investigate the level of management costs, specific fees are not being proposed. For illustration, however, the total funds needed to cover major costs can be judged from the fee schedules established to cover costs associated with foreign fishing. A 1980 amendment to the MFCMA established the requirement that MFCMA-related costs be imposed on foreign fishing companies in proportion to foreign catch as a fraction of total catch in U.S. waters (P.L. 94-265, Sec. 204b(10)). This policy was implemented by establishing permit and poundage fees using a standard formula (including research, management, surveillance, and data collection costs, but not at-sea observer program costs).

During 1982 through 1986 the foreign fee computation procedure remained essentially unchanged, with most of the revenue collected from poundage fees. For example, poundage fees for foreign fishing in the EEZ off Alaska in 1984 came to a total of around $46 million, or about $35.3 per metric ton averaged over 1.3 million metric tons of pollock, Pacific cod, flounders, and other groundfish. Assuming that the management and enforcement costs were reasonably computed, a domestic royalty on groundfish quota shares could be based upon some reasonable proportion of this total tonnage cost. A fifty percent share of costs would lead to a $17.6 royalty per ton. The royalty rate could vary among species to reflect exvessel values of different species, as was the practice in setting foreign fees. More detailed examination of the cost components is needed in order to determine what proportion of total management costs would be reasonable to derive from user fees or quota royalties.

STRATEGY 2

The second strategy differs from the first strategy mostly in steps 1 and 3. The initial allocation of licenses and quota shares in Strategy 1 relied upon past participation and harvest records over the previous several years. In this second strategy there would be no initial license limitation, and the rights to harvest shares would be accumulated through documented harvests over a number of years. Because the upgraded monitoring and enforcement system (Step 2) and the management cost sharing system (Step 4) are equally important to the two strategies, the extensive discussion need not be repeated here. The presentation of Strategy 2 follows the four-step format followed for Strategy 1.

**STEP 1: REGISTER AND DOCUMENT VESSELS AND FISH BUYERS.** The first step is simply to establish a complete and consistent system of registration for owners or prospective owners of groundfish fishing vessels. The registration of vessels would involve little more than a continuation of the existing system operated by the NMFS Alaska Regional Office. The vessel owners would submit necessary information on vessel characteristics (including Coast Guard registration numbers, and radio call letters) and information regarding how management personnel may contact them. Unlike the Strategy 1, this would not constitute a limit to entry of new vessels. Since the licenses would have no market values and would not be limited in number, no transfers of licenses would be anticipated.

Buyers of groundfish would need to be licensed so that records can be kept of all sales and purchases. Foreign and domestic buyers would be required to maintain and periodically submit records of quantity, condition, and species of fish bought. This information would be equivalent to existing State requirements for "fish tickets."

**STEP 2: UPGRADED MONITORING AND ENFORCEMENT.** This step would be essentially identical to Step Two of Strategy 1, except that the enhanced monitoring functions associated with enforcement of ITQs would be phased in over a number of years as the ITQs are issued.

**STEP 3: ALLOCATION OF INDIVIDUAL TRADEABLE QUOTAS.** Individual rights to harvest fish would be established over a period of years, based upon documented performance in the fishery. This would be a variant on the "homestead" concept in which resource ownership rights are given to those demonstrating a commitment to using the resource. The owner of any U.S. registered vessel landing groundfish in the U.S. or catching and processing groundfish in the EEZ would be issued certificates giving perpetual rights to harvest groundfish. These certificates would be individual transferable quota shares designating species, quantity, areas and any other stipulations consistent with fishery management regulations. The harvest rights would be accumulated in the following fashion:

1. During year 1 (for example, assume this is 1989) the fishery proceeds as usual under conventional fishery regulations. Each vessel's harvest would account for a documented portion of the TACs for the year. At the end of the year, each vessel owner would be issued ITQ certificates equal to 20 percent of actual documented TAC shares landed on shore or processed at-sea on U.S. registered vessels. Vessel owners would also be issued ITQ certificates equal to 10 percent of joint venture harvests. Thus a shoreside trawler or a factory trawler would get twice the credit for each ton landed as a joint venture trawler. (This proportion could be negotiated among NPFMC and industry advisors; a two-to-one ratio is used here for illustration.)
2. In year 2, open access fisheries are held for each species, with each species quota equal to the TAC established by NPFMC/NMFS minus the quantity allocated to individuals through ITQs. Holders of ITQs can harvest in accordance with all other pertinent regulations during the open access season and/or during periods of the year when the open access fishery has taken its quota and is closed. The ITQs are transferable via private transaction; transfers must be recorded at the NMFS Regional Office weekly. ITQs are to be used for landing fish at shoreside locations and for processing at sea aboard factory trawlers, U.S. registered motherships, or floating processors. At the end of the year, each vessel owner would be issued additional ITQ certificates equal to 20 percent of actual documented DAP harvest (including both open access and ITQ harvest) and 10 percent of documented JV harvest.
3. In succeeding years, open access fisheries would be held for each species, with quotas equal to the share of TAC not yet allocated in ITQs through the prior year. Holders of ITQs can, as in year 2, harvest during the open access season or during the remainder of the year in accordance with all other fishery regulations. Unless the total allocation would exceed 100 percent of the TAC, vessel owners would continue to receive additional ITQ certificates at the end of each year at the rate of 20 percent for DAP and 10 percent for JV fishing. At the end of any year in which the normal allocation of new ITQs would cause total outstanding shares to exceed 100 percent, the year-end ITQ allocations will be adjusted downward until the total ITQ shares issued just equals 100 percent.

This strategy would eventually allocate out all TACs for groundfish to privately held ITQ certificate holders. If the domestic fishery continues to grow during the five-year allocation period, the JV fishery will decline, and most of the ITQs will be issued to DAP fishermen. To illustrate how this might work, a numerical example has been worked out (Tables 3 and 4). This is not a serious attempt to predict the future course of the fishery. In this example, we assume a constant total TAC of 2.1 million metric tons. We also assume that there is no foreign fishery, that the DAP fishery grows to absorb the entire TAC between 1989 and 1994, and that the JV fishery shrinks to accommodate the DAP fishery. This future course for the groundfish fishery is displayed in Table 3.

Table 3. Hypothetical future groundfish harvests.

| Year | Harvest by Sector<br>JV | <br>DAP | <br>Total |
|---|---|---|---|
| | —thousands of metric tons— | | |
| 1989 | 1200 | 500 | 1700 |
| 1990 | 1000 | 800 | 1800 |
| 1991 | 700 | 1200 | 1900 |
| 1992 | 400 | 1600 | 2000 |
| 1993 | 100 | 2000 | 2100 |
| 1994 | 0 | 2100 | 2100 |
| 1995 | 0 | 2100 | 2100 |

Table 4. Hypothetical ITQs issued during seven-year period.

| Year | New ITQs issued to JVs | Cummulative ITQs to JVs | New ITQs issued to DAP | Cummulative ITQs to DAP | Total ITQs issued |
|---|---|---|---|---|---|
| | —thousands of metric tons— | | | | |
| 1989 | 120 | 120 | 100 | 100 | 220 |
| 1990 | 100 | 220 | 160 | 260 | 480 |
| 1991 | 70 | 290 | 240 | 500 | 790 |
| 1992 | 40 | 330 | 320 | 820 | 1150 |
| 1993 | 10 | 340 | 400 | 1220 | 1560 |
| 1994 | 0 | 340 | 420 | 1640 | 1980 |
| 1995 | 0 | 340 | 120 | 1760 | 2100 |

This scenario assumes ITQs issued to JV vessels equal to 10% of harvest and to DAP vessels equal to 20% of harvest, and that DAP sector expands as indicated in Table 3a.

Given these assumptions, the allocation rules suggested above would lead to the division of quota shares between JV vessel owners and DAP vessel owners displayed in Table 4. By the end of 1993 the JV vessel owners would have accumulated 340 thousands tons of ITQs, while the DAP vessels owners would have 1,220 thousand metric tons of ITQs. After 1993, the domestic sector would take the entire TAC, but the 20% entitlement rule would continue phasing in the ITQ allocations until the end of 1995. In 1995, the last year in which an open access fishery would occur, year-end allocation would constitute only a portion of the earlier 20% of harvest rule.

DISCUSSION OF STEP 3. This step addresses the criteria of fairness in allocation of harvest rights, while adhering to the spirit of the Americanization process, by allowing the competition for fish to determine the ultimate distribution of fishing rights. Several aspects of this approach warrant emphasis:

1. Documented harvests before 1989 would not enter into the allocation of ITQ shares. Using actual harvests during the phase-in allocation period to determine shares, however, would seem to meet the MFCMA requirement that limited access systems take into account the present participation, historical fishing practices in, and dependence on the fishery.
2. This ITQ allocation system gives each groundfish vessel owner a fair chance to accumulate harvest rights, because it opens opportunities to claim quota shares over an extended period of time. Operational or market problems encountered in any given year will not have undue influence on the eventual ITQs accumulated by vessel owners. No vessel active during the period will fail to acquire some harvest rights, although vessels in joint ventures will acquire rights at a reduced rate. Also, additional shares will be available through private transactions; permitting more efficient or profitable firms to expand, and permitting all vessel owners the opportunity to tailor species quota shares to meet their production plans or fishing luck.
3. The rate of growth in the domestic processing industry will determine how quickly the JV fishery shrinks (just as under the current management system), and it will also determine what fraction of the ITQs are eventually issued to JV vessel owners. If many years go by without significant growth in the DAP fishery, the ITQs accumulated through JV fishing may become a large portion of the total TAC. Since these ITQs are supposed to be used for DAP harvests, and are not required for JV fishing, lack of a domestic market could cause these ITQs to remain unutilized. However, so long as the DAP fishery is expected to harvest less than the TAC, a JV allocation would continue to be established each year (just as under the existing groundfish management regime).

**STEP 4: ESTABLISH A SYSTEM OF SHARED FUNDING.** As in Strategy 1, some management costs would be shifted to the private industry through fees and royalties. Because the individual quota shares would be allocated over a number of years under Strategy 2, it would seem reasonable to phase in the user fees in a similar fashion. This could be done by linking the fees to ITQs owned. A fee per ton of ITQ issued, or an ad valorem tax on ITQs owned would accomplish this. An initial issuance fee (e.g., 1 dollar per ton of ITQ) could be combined with an annual fee to assure sufficient funding for management operations before ITQs are actually being used in the fishery.

## Conclusions

Improving the management of groundfish off Alaska can result in increased net economic returns from the commercial fishery, and it can distribute those returns equitably among fishermen and taxpayers, while assuring fish stock conservation and maintaining management and private business flexibility. Conventional regulations can assure conservation of fish stocks, and they can preserve past harvest shares among user groups. To generate the estimated $120 million to $200 million in net economic values, however, requires substantial reform of the harvest rights system. Limiting fishery access through individual quotas shares seems to be the most feasible approach. The paramount concern in establishing a limited access system is equity in the distribution of fishing rights and economic wealth. Additional concerns are (1) accuracy and completeness of scientific and compliance monitoring data, and (2) enforcement of catch and by-catch quotas.

The two illustrative programs of management improvement described above seek to address all of these concerns in a logical sequence. The first strategy starts with a license limitation system for the groundfish fleet, temporarily slowing expansion of the groundfish fleet to provide time for development and implementation of a comprehensive enforcement and data collection system. The second strategy skips the license limitation step. Both strategies require a significant early effort to expand and solidify the management information data base. Without the data provided such a system, neither an individual quota nor the traditional aggregate, open access quota approach can successfully conserve fish stocks.

In both strategies the third step involves the allocation of individual share quotas to licensed fishing vessel owners. The first strategy allocates based upon past harvest shares, and it provides additional shares of under-utilized species to U.S. fishing companies on a first-come, first-served basis. The second strategy sets up a several year phase in period, during which vessel owners gain rights to quota shares by harvesting fish. Both strategies can be structured so that the existing preference for domestic fish processing over joint venture processing is retained. If desired, Americanization of the groundfish industry can be built into a share quota system.

The fourth step of each strategy institutes a user fee system to cover at least that portion of the management costs associated with monitoring and enforcing catch quotas on each vessel. A minimum version of this funding system would be similar to the observer fees system used for the foreign observer program. Profits from fishing operations under an individual share quota system would be more than adequate to pay these fees. The sharing of management costs between taxpayers and commercial fishing companies is consistent with common notions of equity.

The foregoing programs for groundfish management are offered as models for consideration by the North Pacific Fishery Management Council, the Council's advisory committees, and others interested in conservation of groundfish resources. While they clearly require further development in detail, the proposed strategies demonstrate possible ways of achieving the variety of objectives associated with public management and use of the vast groundfish resources in the EEZ off Alaska. Development of more comprehensive and politically feasible management strategies will require intensive efforts involving participation by government officials, management experts, and industry representatives.

The current rate of development in the U.S. fishery offers a relatively small window of opportunity (two years or so, in this authors estimation) for implementing the management institutions needed to assure substantial achievement of the objectives. Conventional management measures are clearly not up to the task. A frequent impediment to adopting limited access, especially individual quota shares, is the fear of uncertain consequences. However, change is inherent in the process of fishery development. The illustrative strategies developed above are a positive attempt to devise an efficient and equitable style of groundfish management.

## Endnotes to Section VI

1. After lengthy discussion and development of an individual quota system for Pacific halibut, the NPFMC proposed a simple moratorium to take effect in June 1983. The moratorium was rejected by NOAA on recommendation of the Director of the Office of Management and Budget who claimed, in part, that it "would not . . . resolve the excess investment problem without creating additional economic problems . . ." and "that an adequate showing has not been made of the need for the lengthy moratorium proposed, and that the moratorium would be likely to delay consideration of alternative measures to resolve the halibut management problem in a fair, lasting, and economically efficient manner." (All quotes taken from Richards and Gorham, 1986; pp 44-48) Different interpretations of this rejection place varying degrees of confidence on the technical versus political underpinnings. Most would agree that the plan was deficient in some respects.

2. The concept of extracting substantial economic rent from the fishery is not pursued further here due to the poor prospects for political support. Rent extraction as such would involve setting fees or sales prices for quota shares at levels high enough to capture most of the potential net economic value of the fishery. Populists and single taxers may applaud the taxation of rents because they fall "upon those who receive from society a peculiar and valuable benefit..." (Henry George, 1953; p. 139) My deletion of the common exhortation to capture rents from a public resource, more or less follows the logic explored by R. Stokes (1986).

   Stokes draws upon the theory of interest group/government interaction devised by Mancur Olsen (1971), to conclude that among efficient public policies the more feasible ones are those that support concentrated as opposed to diffuse interests. In the typical commercial fishery, economic efficiency consequences are essentially the same whether potential profits accrue to owners of quota shares or to the public treasury. Since quota share holders will represent a concentrated interest group whose economic welfare depends upon retaining private title to resource rents, they will strongly oppose a public policy that extracts rent. The beneficiaries of rent taxation, the public at large, is too diffused an interest group to promote its interests effectively against those of the commercial industry. Hence, political feasibility militates against the full taxation proposal. Nevertheless, minimal standards of equity seem to call for collection of fees to allay public fishery management costs.

## References

Anderson, L.G. 1985. Potential economic benefits from gear restrictions and license limitation in fisheries regulation. Land Economics 61(4):409-418.

Bakkala, R.G. and J.W. Balsiger, editors. 1987. Condition of groundfish resources of the eastern Bering sea and Aleutian Islands region in 1986. NOAA Tech. Mem. NMFS F/NWC-117. U.S. Dept. Commerce, NOAA. Seattle, WA. 187 p.

Berger, J.D., J.E. Smoker, and K.A. King. 1986. Foreign and joint venture catches and allocations in the Pacific northwest and Alaska fishing area under the Magnuson Fishery Conservation and Management Act, 1977-84. NOAA Tech. Mem. NMFS F/NWC-99. Seattle.

Burke, W.T. 1977. Recapture of economic rent under the FCMA: Sections 303-304 on permits and fees. Washington Law Review 52:681-700.

Clancy, T.J. and R.E. Nelson, Jr. 1987. Provisional summary of U.S. observer activities and foreign and joint venture fisheries in the northeast Pacific ocean and eastern Bering Sea, 1986. NWAFC Processed Report 97-12. NOAA. NMFS, Seattle, WA. 43 p.

Food and Agriculture Organization (FAO). 1987. Yearbook of fishery statistics 1985. Vol. 60. Rome, Italy.

Fraser, G.A. 1978. License limitation in the British Columbia salmon fishery. Pages 358-381 in R.B. Rettig and J.J.C. Ginter (eds.).

Fredin, R.A. 1987. History of regulation of Alaska groundfish fisheries. NWAFC Processed Report 97-07. NOAA, NMFS, Seattle, WA. 63 p.

Gulf of Alaska Groundfish Plan Team. 1986. Resource Assessment Document for the Gulf of Alaska groundfish fishery. Prepared for the North Pacific Fishery Management Council (November, 21). Anchorage, AK. 73 p.

Hanna, S. and W. Silverthorne. 1987. Interaction within existing management measures. Pages 19-22 in D.D. Huppert (ed.).

Huppert, D.D., editor. 1987. Limited access alternatives for the Pacific groundfish fishery. NOAA Tech. Rep. NMFS 52. U.S. Dept. Commerce, NOAA, Seattle, WA. 45 p.

Huppert, D.D. and D. Squires. 1987. Potential economic benefits and optimum fleet size in the Pacific coast trawl fleet. Marine Resource Economics 3(4):297-318.

Major, R.L., editor. 1987. Condition of groundfish resources of the Gulf of Alaska region as assessed in 1986. NOAA Tech. Mem. NMFS F/NWC-119. U.S. Dept. Commerce, NOAA, Seattle, WA. 204 p.

Mollett, N., editor. 1986. Fishery access control programs worldwide: proceedings of the workshop on management options for the north Pacific longline fisheries. Alaska Sea Grant Report No. 86-4. University of Alaska, Fairbanks, Alaska.

National Marine Fisheries Service. 1985. Fish and Chips. Office of Industry Services, International Trade Staff Report 85-1. Washington, D.C. 8 p.

North Pacific Fishery Management Council. 1984. Fishery management plan for the Gulf of Alaska groundfish fishery (incorporating amendments 1 through 11 and 13). Anchorage, AK.

North Pacific Fishery Management Council. 1986. Fishery management plan for the Bering Sea/Aleutian Islands groundfish (Incorporating amendments 1 through 9). Anchorage, AK.

Olsen, M. 1972. The Logic of Collective Action. Harvard Univ. Press, Cambridge, Mass.

Pierce, P.H. 1982. Turning the tide: a new policy for Canada's Pacific fisheries. Canadian Department of Fisheries and Oceans, Ottawa, Canada.

Rettig, R.B. 1984. License limitation in the United States and Canada: an assessment. N. Amer. J. Fish. Mgmt. 4:231-248.

Rettig, R.B. and J.J.C. Ginter, editors. 1978. Limited Entry as a Fishery Management Tool. University of Washington Press, Seattle, Washington.

Richards, H. and A. Gorham. 1986. The demise of the U.S. halibut fishery moratorium: a review of the controversy. Pages 33-54 in Mollet, (ed.).

Rolph, E. 1983. Government allocation of property rights: Who gets what? J. Policy Analysis Mgmt. 3(1):45-61.

Ruddle, K. 1987. Administration and conflict management in Japanese coastal fisheries. FAO Fish. Tech. Rep. 273. Rome, Italy. 93 p.

Schelle, K. and B. Muse. 1986. Efficiency and distributional aspects of Alaska's limited entry program. Pages 317-352 in Mollet (ed.).

Stokes, R.L. 1983. Limited Entry in the Pacific Halibut Fishery: the Individual Quota Option. Council Doc. #20. Anchorage:North Pacific Fishery Management Council.

Stokes, R.L. 1986. Improving the relevance of fisheries economics through political analysis: Some suggested approaches. Pages 42-58 in E. Miles, R. Pealy and R. Stokes (eds.), Natural Resources, Economics and Policy Applications. Univ. Washington Press, Seattle, WA.

Sturgess, N.H. and T.F. Meany, editors. 1982. Policy and practice in fisheries management. Australian government Publishing Service, Canberra, Australia.

# APPENDIX

## Computation of Optimum Factory Trawl/Mothership Fleet and Potential Economic Return from Bering Sea/Aleutian Islands Fishery

The objective of this computation is to determine number and type of fishing vessels needed in a factory trawler/mothership fleet to harvest the total allowable catches of BSAI groundfish. As noted in the text of Section II, and further explained in Huppert and Squires (1987), any such calculation is contingent on the data and assumptions used. Because broad assumptions and preliminary estimates are incorporated along with more precise information, the results are considered suggestive rather than conclusive. This Appendix lays out all the assumptions, so that those willing to dig into the details may develop interpretations of the model and results that are consistent with the data and assumptions.

Linear programming (LP) is a standard operations research technique that maximizes a linear objective function subject to a set of linear inequality constraints. A solution to an LP consists of the calculated optimum level of all variables affecting the objective function. In this application, net economic return (i.e. total groundfish product value minus fishing and processing cost) is the objective. Requiring that the sum of the catch across vessel classes for each species is no greater than the total allowable catch represents a set of linear inequality constraints. Each solution to the trawl fleet model involves determining the number of vessels in each of five classes of trawlers and motherships, and determining how to deploy the potential fishing days of this fleet across various species targeting modes and areas in the BSAI. Each possible fleet size and deployment pattern generates a set of catches, which result in a set of fish product quantities, product values, fishing and processing costs, and fixed costs. The linear programming method finds the single combination of vessel numbers and fishing day allocations that achieves the highest possible net economic value. Each part of the computation involves the data summarized in the Tables below. In order to assure than the number of vessels in the solution is an integer, we use a special version of the linear programming algorithm, called mixed integer programming. These computations were performed on a microcomputer using the LP/MIP83©, Version 5.00 program (copyrighted by Sunset Software, San Marino, California).

Net economic return for each vessel class (described in Table 1), fishing mode, and area is computed in several stages. First, the quantities caught by a vessel of any given class are computed by multiplying days of operation times the species-specific rates of catch or processing. Second, catch quantities are allocated to fish product classes (Table 2). Third, quantities of fish products are calculated by multiplying catch quantities by product yield rates (product weight divided by raw fish weight, Table 3). Fourth, revenues are equal to product quantities multiplied by product prices (Table 4). Fifth, these dollar values are summed over all species caught by all vessels, in all areas, and all modes of operation, creating a gross product value per day of operation. Sixth, the variable costs per day of operation (Table 1) are subtracted from each gross product value per day to form a variable net return per day.

For any given fleet size and fishing effort deployment, the net returns are summed across all days fished, and the annual fixed costs per vessel are subtracted, yielding a net economic value for the year in each vessel class. Annual fleet-wide net economic return (equivalent to profit) is the sum of the returns from all vessel classes.

The primary data requirements are (1) catch rates by vessel class, area, and target fishery; (2) vessel operating and fixed costs; (3) allocations of raw fish to product categories; (4) product yields; (5) product prices; (6) constraints on total catches by species and area; and (7) limits on number of operating days per year for vessels in each class.

For simplicity, the term "catch rate" is used for both trawlers and motherships, recognizing that mothership "catch" rates actually represent processing plant use and catcher vessel delivery rates. Catch rates for small and medium factory trawlers were computed using weekly reports compiled by the NMFS Alaska Regional Office during 1986 and 1987 (through mid-August). Catch rates have been calculated from foreign vessel observer data from 1986 and 1987 (through mid-August), using data files made available to us by R. Nelson of NMFS' Northwest and Alaska Fisheries Center. The catch rates are computed for each species target mode by assigning fishing days to target categories based upon predominance of species reported (highest percent in catch).

Additional modifications to the computed average catch rates and fishing seasons were incorporated based upon the author's subjective judgements. The two main adjustments were to walleye pollock catch by large motherships and Pacific cod catch rates by medium factory trawlers. In each case, the adjustment to computed data was deemed necessary to obtain reasonable results from the model. First, pollock catch rates for Class 5 motherships were reduced from 620-670 metric tons per day to 500 tons per day in the main fishing zones (Areas I and II in the Bering Sea). This adjusted catch rate is more in line with capacity limits for 460-foot mothership operations as projected by Natural Resources Consultants (1984b). Second, in preliminary runs of the LP model, the high computed Pacific cod catch rate for medium factory trawlers (about 42 mt/day in area I) led to a solution in which 22 medium trawlers were assigned to Pacific cod fishing, resulting in huge and probably unrealistic profits. This result was considered unrealistic because it ignores the marked seasonality in Pacific cod availability to trawl gear. Based upon monthly Pacific cod trawl catch information (Bakkala and Balsiger, eds.; p. 41), it was determined that the really high catch rates can be reliably obtained for only about four months per year. To incorporate this seasonal factor, an additional constraint was added that permits the high-yield Pacific cod fishery to occur for only four months per year. Pacific cod catch rates for other vessel classes and in non-Pacific cod targetting modes were not adjusted. These were the only two departures from the straightforward use of computed average catch rates in the linear programming model.

Costs of operating the fleet are divided into variable and fixed. Variable costs are further subdivided into those cost elements that accrue during vessel operations independently of actual catch processed and those that increase with quantity or type of fish processed. The "catch independent" variable costs include fuel, groceries, supplies, repair and maintenance, crew payments, and crew transportation. Catch dependent variable costs include packaging, freight and distribution costs, storage, additives to surimi, duties for fish exported, and, most importantly, payments by motherships to catcher vessels. Fixed costs include interest costs (based upon vessel value), hull insurance, overhead, and P & I insurance. The data used in this model are derived from diverse sources; including Natural Resources Consultants, 1984 (July), various cost data sheets available from the Northwest and Alaska Fisheries Center, and direct interviews with industry members. Several cost elements (fuel price, insurance rates, interest rates) were updated to values appropriate to 1987. All of the underlying information, in the format of cost summaries, are listed at the end of the Appendix. Use of subjective judgements in establishing these cost elements is unavoidable, and the reader should be aware that the results of the computations are sensitive to the assumed costs, prices, and other parameters.

Product prices (Table 4) and product yields (Table 3) are derived from several sources; including NMFS' Market News, reports of joint venture companies summarized by NMFS' Alaska Regional Office, and various personal contacts. Allocations of fish across product categories (Table 2) are based upon the same sources as cost information, with the addition of various judgements based upon discussions of fishing strategy with fishing industry members.

The total catch constraints used in the linear program represent recent estimates of Acceptable Biological Catches (ABCs) for 1988, and percentage distributions of catch across regulatory areas are based upon actual distributions from 1986 through mid-August, 1987 (Table 5). Maximum assumed days fishing per year for each vessel class (Table 1) are derived from NRC (1984), confidential information supplied by the Northwest and Alaska Fisheries Center, and personal communications.

The basic solution to the linear programming model is displayed in Table 6. In this solution, the program is forced to include at least one vessel in each class. This solution delineates the following optimal factory trawler and mothership groundfish fleet in the Bering sea: (1) a total of 34 processing vessels are needed -- 1 small factory trawler, 3 medium factory trawlers, 21 large factory trawlers, 6 fillet motherships, and 3 large surimi motherships (2) a total of 1,741,812 metric tons of groundfish would be harvested, (3) the processed products would be worth roughly $884 million, (4) the net profit from this operation would be $124 million, and (5) 1,195,792 metric tons of the total ABCs would not be harvested. Given that catcher vessels supplying the motherships can harvest 16,000 to 18,000 metric tons per year (NRC, 1984b; p. 9), the associated catcher fleet will need to contain 44 to 49 vessels.

The second run of the linear program (Table 7) was intended to reveal whether the economic and catch data entered was consistent with each vessel class being a potentially profitable operation. In this run all data and constraints remain as before except that the fleet is limited to one vessel of each type. The solution to this LP, while not representing an answer to how large the fleet should be, shows that each vessel class is potentially profitable. The reason that the optimal solution to fleet size (Table 6) includes only one Class 1 vessel is not that such vessels cannot be profitable, but the fish can be caught more profitably by the other types of vessels. This conclusion is dependent upon the species mixes and catch rates assigned to each vessel class. Because the catch rates by species for each class of vessel are important variables, additional work may be warranted to assure that the assumed catches are consistent with the increasing experience with U.S. factory trawlers.

The results depicted in Table 8 represent the base economic assumptions and catch constraints, but with the deletion of class 5 motherships from the model. With this additional constraint, the optimum fleet would include just a few more large factory trawlers and small fillet mothership operations, but would be smaller overall. The total catch drops to 1.48 million metric tons, gross value of product drops to $747 million, and the aggregate economic fleet profit decreases to $98 million.

The next two Tables reflect the basic model assumptions again (i.e. no special constraints on number of vessels) but with all fish product prices alternately increased and decreased by 20 percent. The hypothetical increase in prices results in only 1 additional large factory trawler in the optimum fleet, while the net profit from the groundfish fleet operation would increase to $281 million per year. As shown in Table 10, a decrease of 20 percent in all prices would cause a radical decline in the optimum fleet to only 13 vessels with an annual profit of $3.3 million. Clearly, the extreme sensitivity of optimum fleet size to a twenty percent price reduction is a result of model assumptions, particularly the fixed cost levels.

The results of this linear programming model cannot be taken as definitive proof that any particular processor fleet configuration is best. It is also wrong to take the profits for a given class of vessel shown in the LP solution as estimates of profits actually being earned by U.S. groundfish vessels. Each vessel in operation has unique characteristics and fishing patterns that deviate somewhat from any of the vessel classes characterized in this analysis. And, more importantly, the profits computed here are consistent with efficient fleet investment and deployment, something that has never been tried in a U.S. groundfish fishery. The underlying assumption is that no excess fishing capacity will be built. Under existing fishery institutions, a much larger fleet will be built, with each additional vessel providing a return on investment to its owners. This is simply a restatement of the usual conclusion that open access to fishing draws excessive fishing capacity causing a reduction in overall profit (resource rents). While a rational central planner, or a competitive fishery having quantitative harvest rights, might develop an optimum fleet, a competitive fishery with open access to the fish stock would not.

This is a provisional model. Various cost and price assumptions need to be checked further, and the catch rates and product allocations may require verification. The parameter values used in the model are accurate enough, however, to support general conclusions. First, mothership operations appear to be profitable, but large factory trawlers also have an important place in harvesting and processing pollock. Also, the fleet needed to exploit the Bering sea groundfish efficiently, is much smaller in number than the fleet that has been operating there in foreign and joint venture fisheries. Finally, total potential profits from the fishery are large enough to warrant extensive public interest and participation in the development of efficient fishery management programs.

## References

Bakkala, R.G. and J.W. Balsiger, editors. 1987. Condition of groundfish resources of the eastern Bering sea and Aleutian Islands region in 1986. NOAA Tech. Mem. NMFS F/NWC-117. U.S. Dept. Commerce, NOAA. Seattle, WA. 187 p.

Huppert, D.D. and D. Squires. 1987. Potential economic benefits and optimum fleet size in the Pacific coast trawl fleet. Marine Resource Economics 3(4):297-318.

Natural Resources Consultants. 1984. Operations and economics of selected Alaska groundfish fisheries. North Pacific Fishery Management Council Document #28. Anchorage, AK.

Appendix Table 1. Descriptions and assumed operating and fixed costs per vessel in each class.

| | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 |
|---|---|---|---|---|---|
| Description | Factory Trawler | Factory Trawler | Factory Trawler | Mother-ship | Mother-ship |
| Length (feet) | 162 | 200 | 300 | 300 | 460 |
| Crew Size | 25 | 38 | 85 | 85 | 300 |
| Max. operating days: At-sea | 220 | 260 | 300 | 300 | 320 |
| Processing or fishing | 220 | 260 | 265 | 265 | 265 |
| Fixed costs per year[1] ($1,000s) | $1,736 | $3,376 | $6,784 | $8,032 | $11,556 |
| Variable cost[2] | | | | | |
| 1. Daily - catch indep. | $11,550 | $27,077 | $32,323 | $24,906 | $59,683 |
| 2. Cost per MT caught | $47.3 | 55.6 | 68.10 | 221.89 | 203.89 |

[1] The major items of fixed cost are cost of capital investment, hull insurance, and P & I insurance. Rather than estimate loan costs, opportunity cost of owner's equity, and depreciation; we have included a single cost of capital investment equal to the annual payment on a 10%, 15-year loan for the original vessel price.

[2] Variable costs are divided into (1) those that accrue daily as the vessel operates at sea, and (2) those that are incurred only as fish are processed. The first group includes fuel, groceries, fishing gear, repair and maintenance, and crew payments. Crew payments are treated like wages and salaries rather than as shares in these computations. The second set of variable costs includes packaging, freight & distribution, storage, and fish purchases on motherships. At-sea fish purchase prices are assumed to be $132/mt for pollock and $236/mt for Pacific cod. While the catch-related variable cost depends upon the actual catch per day the costs reported above are averages based upon the calculated average cost per mt ton from the linear programming solution listed in Table 8 below.

Appendix Table 2. Allocation of catch to various product categories.

| | Roe | Surimi | Fillet | Block | H & G |
|---|---|---|---|---|---|
| 1. Small Trawlers | | | | | |
| Pollock | 0 | 0 | 100 | 0 | 0 |
| Cod | 0 | 0 | 100 | 0 | 0 |
| Yellowfin Sole | 0 | 0 | 0 | 0 | 100 |
| Other Flatfish | 0 | 0 | 0 | 0 | 100 |
| Sablefish | 0 | 0 | 0 | 0 | 100 |
| Rockfish (including POP) | 0 | 0 | 0 | 0 | 100 |
| Atka Mackerel | 0 | 0 | 0 | 0 | 100 |
| Other groundfish | 0 | 0 | 0 | 0 | 100 |
| 2. Medium Trawlers: | | | | | |
| Pollock | 0 | 0 | 100 | 0 | 0 |
| Cod | 0 | 0 | 100 | 0 | 0 |
| Yellowfin Sole | 0 | 0 | 0 | 0 | 100 |
| Other Flatfish | 0 | 0 | 0 | 0 | 100 |
| Sablefish | 0 | 0 | 0 | 0 | 100 |
| Rockfish (including POP) | 0 | 0 | 0 | 0 | 100 |
| Atka Mackerel | 0 | 0 | 0 | 0 | 100 |
| Other groundfish | 0 | 0 | 0 | 0 | 100 |
| 3. Large Trawlers | | | | | |
| Pollock | 30 | 60 | 20 | 12 | 0 |
| Cod | 0 | 0 | 35 | 35 | 30 |
| Yellowfin Sole | 0 | 0 | 0 | 0 | 100 |
| Other Flatfish | 0 | 0 | 0 | 0 | 100 |
| Sablefish | 0 | 0 | 0 | 0 | 100 |
| Rockfish (including POP) | 0 | 0 | 0 | 0 | 100 |
| Atka Mackerel | 0 | 0 | 0 | 0 | 100 |
| Other groundfish | 0 | 0 | 0 | 0 | 100 |
| Small (Fillet) Mothership | | | | | |
| Pollock | 30 | 0 | 78 | 12 | 0 |
| Cod | 0 | 0 | 35 | 35 | 30 |
| Yellowfin Sole | 0 | 0 | 0 | 0 | 100 |
| Other Flatfish | 0 | 0 | 0 | 0 | 100 |
| Sablefish | 0 | 0 | 0 | 0 | 100 |
| Rockfish (including POP) | 0 | 0 | 0 | 0 | 100 |
| Atka Mackerel | 0 | 0 | 0 | 0 | 100 |
| Other groundfish | 0 | 0 | 0 | 0 | 100 |

Appendix Table 2. Allocation of catch to various product categories - cont'd.

| | Roe | Surimi | Fillet | Block | H & G |
|---|---|---|---|---|---|
| Large (Surimi) Mothership | | | | | |
| Pollock | 30 | 80 | 0 | 12 | 0 |
| Cod | 0 | 0 | 35 | 35 | 30 |
| Yellowfin Sole | 0 | 0 | 0 | 0 | 100 |
| Other Flatfish | 0 | 0 | 0 | 0 | 100 |
| Sablefish | 0 | 0 | 0 | 0 | 100 |
| Rockfish (including POP) | 0 | 0 | 0 | 0 | 100 |
| Atka Mackerel | 0 | 0 | 0 | 0 | 100 |
| Other groundfish | 0 | 0 | 0 | 0 | 100 |

Appendix Table 3. Product yields.

| Product | Percent |
|---|---|
| Pollock Surimi | 23.00% |
| Pollock Roe | 3.00%* |
| Pollock Fillets | 20.00% |
| Pollock Blocks | 20.00% |
| Cod Fillets | 20.00% |
| Headed & Gutted Cod | 50.00% |
| Headed & Gutted YFsole | 80.00% |
| Headed & Gutted Flatfish | 75.00% |
| Headed & Gutted Sablefish | 65.00% |
| Headed & Gutted Rockfish | 50.00% |
| Headed & Gutted Other SP. | 75.00% |

*Roe yield applied to all pollock caught in roe fishery, i.e. about 30% of pollock catch.

Appendix Table 4. Assumed prices for groundfish products.

| Fish Product | $/lb | $/metric ton |
|---|---|---|
| Surimi | 1.00 | 2206 |
| Pollock Roe | 2.40 | 5291 |
| Pollock Fillets | 1.00 | 2204 |
| Pollock Blocks | 1.00 | 2204 |
| Cod Fillets | 1.90 | 4189 |
| Headed & Gutted Cod | 0.72 | 1786 |
| Headed & Gutted Flatfish | 0.47 | 1036 |
| Headed & Gutted Sablefish | 1.35 | 2976 |
| Headed & Gutted Rockfish | 1.14 | 2513 |
| Headed & Gutted Other | 0.40 | 882 |

Appendix Table 5. Catch limits based upon 1988 ABC and allocation of ABCs across regulatory areas in the Bering Sea.

| Species and Area | MSY Total | Percent |
|---|---|---|
| * Pollock | 1,660,000 | 100.00% |
| Area 1 | 1,119,026 | 67.41% |
| Area 2 | 504,819 | 30.41% |
| Area 4 | 36,155 | 2.18% |
| * Pacific cod | 385,300 | 100.00% |
| Area 1 | 288,097 | 74.77% |
| Area 2 | 37,274 | 9.67% |
| Area 4 | 59,935 | 15.56% |
| * Yellowfin sole | 254,000 | 100.00% |
| Area 1 | 253,478 | 99.79% |
| Area 2 | 488 | 0.19% |
| Area 4 | 33 | 0.01% |
| * Sablefish | 12,200 | 100.00% |
| Area 1 | 351 | 2.87% |
| Area 2 | 0 | 0.00% |
| Area 4 | 11,850 | 97.13% |
| * Atka Mackerel | 21,000 | 100.00% |
| Area 1 | 158 | 0.75% |
| Area 2 | 2 | 0.01% |
| Area 4 | 20,839 | 99.24% |
| * Other Flatfish | 455,500 | 100.00% |
| Area 1 | 377,334 | 82.84% |
| Area 2 | 73,137 | 16.06% |
| Area 4 | 5,029 | 1.10% |
| * Rockfish | 24,100 | 100.00% |
| Area 1 | 618 | 2.57% |
| Area 2 | 1,930 | 8.01% |
| Area 4 | 21,552 | 89.43% |
| * Other Groundfish | 64,000 | 100.00% |
| Area 1 | 43,720 | 68.31% |
| Area 2 | 8,818 | 13.78% |
| Area 4 | 11,462 | 17.91% |

Appendix Table 6. Linear program solution for base assumptions.

| | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 | Totals |
|---|---|---|---|---|---|---|
| | | | Metric tons | | | |
| Pollock | 0 | 3715 | 834750 | 381695 | 397500 | 1617661 |
| Pacific cod | 491 | 35645 | 44520 | 4420 | 2255 | 87332 |
| Yellowfin sole | 0 | 4 | 8081 | 48 | 6 | 8138 |
| Sablefish | 461 | 334 | 323 | 0 | 0 | 1119 |
| Atka mackerel | 0 | 0 | 0 | 0 | 2 | 2 |
| Other flatfish | 120 | 4476 | 14583 | 1988 | 129 | 21295 |
| Rockfish | 1536 | 5 | 172 | 64 | 5 | 1781 |
| Other | 0 | 10 | 3663 | 684 | 127 | 4484 |
| Total catch | 2610 | 44189 | 906092 | 388898 | 400024 | 1741812 |
| No. of vessels | 1 | 3 | 21 | 6 | 3 | 34 |
| | | | $1,000s | | | |
| Gross revenue | 3537 | 37408 | 462246 | 185900 | 194836 | 883929 |
| Variable costs | 2648 | 23577 | 241581 | 125892 | 128967 | 522665 |
| Fixed costs | 1736 | 10128 | 142468 | 48193 | 34669 | 237195 |
| Total costs | 4384 | 33705 | 384050 | 174086 | 163636 | 759860 |
| Net revenue | -846 | 3703 | 78197 | 11815 | 31200 | 124068 |
| Revenue per vessel | $3,537 | $12,469 | $22,012 | $30,983 | $64,945 | $25,998 |
| Profit per vessel | ($846) | $1,234 | $3,724 | $1,969 | $10,400 | $ 3,649 |

Appendix Table 7. Linear program solution with one vessel in each class.

| | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 | Totals |
|---|---|---|---|---|---|---|
| | | | Metric tons | | | |
| Pollock | 54 | 1238 | 39750 | 63616 | 132500 | 237158 |
| Pacific Cod | 584 | 11882 | 2120 | 737 | 904 | 16226 |
| Yellowfin Sole | 0 | 1 | 385 | 8 | 0 | 394 |
| Sablefish | 390 | 111 | 15 | 0 | 0 | 517 |
| Atka Mackerel | 0 | 0 | 0 | 0 | 2 | 2 |
| Other Flatfish | 2452 | 1492 | 694 | 331 | 60 | 5030 |
| Rockfish | 269 | 2 | 8 | 11 | 5 | 294 |
| Other | 14 | 3 | 174 | 114 | 58 | 364 |
| Total catch | 3764 | 14730 | 43147 | 64816 | 133529 | 259986 |
| No. of Vessels | 1 | 1 | 1 | 1 | 1 | 5 |
| | | | $1,000s | | | |
| Gross revenue | 4820 | 12469 | 22012 | 30983 | 65096 | 135381 |
| Variable costs | 2719 | 7859 | 11504 | 20982 | 43041 | 86105 |
| Fixed costs | 1736 | 3376 | 6784 | 8032 | 11556 | 31485 |
| Total Costs | 4455 | 11235 | 18288 | 29014 | 54597 | 117590 |
| Net revenue | 365 | 1234 | 3724 | 1969 | 10499 | 17791 |
| Revenue per vessel | $4,820 | $12,469 | $22,012 | $30,983 | $65,096 | $27,076 |
| Profit per vessel | $365 | $1,234 | $3,724 | $1,969 | $10,499 | $3,558 |

Appendix Table 8. Linear program solution with no Class 5 vessels.

| | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 | Totals |
|---|---|---|---|---|---|---|
| | Metric tons | | | | | |
| Pollock | 1 | 1238 | 874500 | 507752 | 0 | 1383490 |
| Pacific Cod | 491 | 11882 | 46640 | 5909 | 0 | 64922 |
| Yellowfin sole | 0 | 1 | 8466 | 86 | 0 | 8553 |
| Sablefish | 461 | 111 | 339 | 0 | 0 | 911 |
| Atka mackerel | 0 | 0 | 0 | 0 | 0 | 0 |
| Other flatfish | 123 | 1492 | 15277 | 2659 | 0 | 19551 |
| Rockfish | 1535 | 2 | 180 | 84 | 0 | 1800 |
| Other | 0 | 3 | 3838 | 911 | 0 | 4752 |
| Total catch | 2611 | 14730 | 949239 | 517400 | 0 | 1483980 |
| No. of vessels | 1 | 1 | 22 | 8 | 0 | 32 |
| | $1,000s | | | | | |
| Gross revenue | 3539 | 12469 | 484258 | 247347 | 0 | 747614 |
| Variable costs | 2648 | 7859 | 253085 | 167615 | 0 | 431206 |
| Fixed costs | 1736 | 3376 | 149253 | 64258 | 0 | 218623 |
| Total costs | 4384 | 11235 | 402338 | 231872 | 0 | 649829 |
| Net revenue | -845 | 1234 | 81920 | 15475 | 0 | 97785 |
| Revenue per vessel | $3,539 | $12,469 | $22,012 | $30,918 | | $23,363 |
| Profit per vessel | ($845) | $1,234 | $3,724 | $1,934 | | $ 3,056 |

Appendix Table 9. Linear program solution with all fish prices increased by 20%.

| | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 | Totals |
|---|---|---|---|---|---|---|
| | Metric tons | | | | | |
| Pollock | 0 | 3715 | 847817 | 381695 | 394863 | 1628091 |
| Pacific cod | 490 | 35645 | 47669 | 4420 | 2267 | 90492 |
| Yellowfin sole | 0 | 4 | 9876 | 48 | 5 | 9933 |
| Sablefish | 462 | 334 | 326 | 0 | 0 | 1122 |
| Atka mackerel | 0 | 0 | 0 | 0 | 3 | 3 |
| Other flatfish | 100 | 4476 | 20406 | 1988 | 129 | 27099 |
| Rockfish | 1548 | 5 | 175 | 64 | 5 | 1795 |
| Other | 0 | 10 | 4176 | 684 | 133 | 5003 |
| Total catch | 2599 | 44189 | 930445 | 388898 | 397407 | 1763538 |
| No. of vessels | 1 | 3 | 22 | 6 | 3 | 35 |
| | $1,000s | | | | | |
| Gross revenue | 4231 | 44890 | 573341 | 223080 | 232285 | 1077828 |
| Variable costs | 2647 | 23577 | 251410 | 136340 | 139003 | 552977 |
| Fixed costs | 1736 | 10128 | 149253 | 48193 | 34669 | 243979 |
| Total costs | 4383 | 33705 | 400663 | 184533 | 173672 | 796956 |
| Net revenue | -152 | 11185 | 172679 | 38547 | 58614 | 280872 |
| Revenue per vessel | $4,231 | $14,963 | $26,061 | $37,180 | $77,428 | $30,795 |
| Profit per vessel | ($152) | $3,728 | $7,849 | $6,424 | $19,538 | $8,025 |

Appendix Table 10. Linear program solution with all fish prices decreased by 20%.

| | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 | Totals |
|---|---|---|---|---|---|---|
| | Metric tons | | | | | |
| Pollock | 54 | 1238 | 39750 | 63616 | 1192500 | 1297158 |
| Pacific cod | 584 | 11882 | 2120 | 737 | 6310 | 21632 |
| Yellowfin sole | 0 | 1 | 385 | 8 | 21 | 415 |
| Sablefish | 390 | 111 | 15 | 0 | 0 | 517 |
| Atka mackerel | 0 | 0 | 0 | 0 | 2 | 2 |
| Other flatfish | 2452 | 1492 | 694 | 331 | 336 | 5306 |
| Rockfish | 269 | 2 | 8 | 11 | 5 | 294 |
| Other | 14 | 3 | 174 | 114 | 334 | 639 |
| Total catch | 3764 | 14730 | 43147 | 64816 | 1199508 | 1325965 |
| No. of vessels | 1 | 1 | 1 | 1 | 9 | 13 |
| | $1,000s | | | | | |
| Gross revenue | 3856 | 9976 | 17609 | 24787 | 467246 | 523474 |
| Variable costs | 2719 | 7859 | 11504 | 19241 | 354867 | 396190 |
| Fixed costs | 1736 | 3376 | 6784 | 8032 | 104007 | 123935 |
| Total costs | 4455 | 11235 | 18288 | 27273 | 458874 | 520125 |
| Net revenue | -599 | -1260 | -679 | -2486 | 8372 | 3348 |
| Revenue per vessel | $3,856 | $9,976 | $17,609 | $24,787 | $51,916 | $40,267 |
| Profit per vessel | ($599) | ($1,260) | ($679) | ($2,486) | $930 | $ 258 |

Appendix Table 11. General cost assumptions

| | |
|---|---|
| Price of Fuel per Gallon | 0.80 |
| Groceries per crewman/day | 15.00 |
| Packaging: | |
| Surimi / lb | 0.01 |
| Fillet & Roe / lb | 0.03 |
| Freight & Distribution: | |
| Surimi & Roe / lb | 0.07 |
| Fillets / lb | 0.11 |
| Storage | 0.02 |
| Crew Transportation: | |
| Trip/Crewman/Year | 1.50 |
| Average Trip Cost | 1,200.00 |
| Surimi Additives/mt | 75.00 |
| Duty /lb | 0.05 |

Appendix Table 12. Small Factory Trawlers.

| | |
|---|---|
| Length | 162 feet |
| Crew size | 25 |
| **Fixed Costs** | |
| Vessel value | $7,500,000 |
| Interest rate | 10.00% |
| Length of loan (years) | 15 |
| Capital costs | $ 986,053 |
| Hull insurance rate | 6.00% |
| Hull insurance cost | $ 450,000 |
| P & I rate/crew man | $ 8,000 |
| P & I cost | $ 200,000 |
| Overhead | $ 100,000 |
| Total annual fixed cost | $1,736,053 |
| **Variable Costs** (Catch independent) | |
| Fuel | $ 600,000 |
| Repair & maintenance | 350,000 |
| Crew transportation | 36,000 |
| Fishing gear | 115,000 |
| Crew salaries | $1,440,000 |
| Total variable costs | $2,541,000 |
| Variable cost per day | $ 11,550 |

Appendix Table 13. Medium factory trawlers.

| | |
|---|---|
| Length | 200 feet |
| Crew size | 38 |
| **Fixed Costs** | |
| Vessel value | $15,000,000 |
| Interest rate | 10.00% |
| Length of loan (years) | 15 |
| Capital costs | $1,972,107 |
| Hull insurance rate | 6.00% |
| Hull insurance cost | $ 900,000 |
| P & I rate/ crewman | 8,000 |
| P & I cost | $ 304,000 |
| Overhead | $ 200,000 |
| Total annual fixed cost | $3,376,107 |
| **Variable Costs** (Catch independent) | |
| Fuel | $ 900,000 |
| Groceries | 100,000 |
| Repair & maintenance | 350,000 |
| Crew transportation | 70,000 |
| Fishing gear | 120,000 |
| Crew salaries | $5,500,000 |
| Total variable costs | $7,040,000 |
| Variable cost per day | $ 27,077 |

Appendix Table 14. Large factory trawlers.

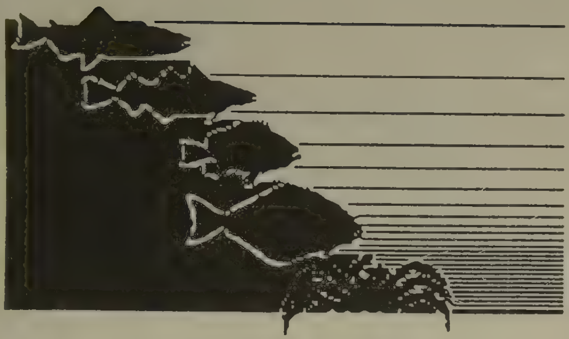
| | |
|---|---|
| Length | 300 feet |
| Crew size | 85 |
| **Fixed Costs** | |
| Vessel value | $30,000,000 |
| Interest rate | 10.00% |
| Length of loan (years) | 15 |
| Capital cost | $3,944,213 |
| Hull insurance rate | 6.00% |
| Hull insurance cost | $1,800,000 |
| P & I rate/crewman | 8,000 |
| P & I cost | $ 680,000 |
| Overhead | 360,000 |
| Total annual fixed cost | $6,784,213 |
| **Variable Costs** (Catch independent) | |
| Fuel rate/Oper. day (gl) | 4,650 |
| Fuel costs | 1,395,000 |
| Groceries | 382,500 |
| Production supplies | 35,000 |
| Repair & maintenance | 400,000 |
| Crew transportation | 153,000 |
| Fishing gear | 200,000 |
| Crew salaries | $6,000,000 |
| Total Variable Costs | $8,565,500 |
| Variable Costs Per Day | $ 32,323 |

Appendix Table 15. Fillet (small) mothership.

| | |
|---|---|
| Length | 300 feet |
| Crew size | 100 |
| **Fixed Costs** | |
| Vessel value | $ 30,000,000 |
| Interest rate | 10.00% |
| Length of loan (years) | 15 |
| Capital cost | $3,944,213 |
| Hull insurance rate | 6.00% |
| Hull insurance cost | $1,800,000 |
| P & I rate/crewman | 8,000 |
| P & I cost | $ 800,000 |
| Overhead | $1,488,000 |
| Total annual fixed cost | $8,032,213 |
| **Variable Costs** (Catch independent) | |
| Fuel rate/Oper. day (gl) | 3,000 |
| Fuel | $ 900,000 |
| Groceries | 450,000 |
| Production supplies | 35,000 |
| Repair & maintenance | 635,000 |
| Crew transportation | 180,000 |
| Crew salaries | $4,400,000 |
| Total variable costs | $6,600,000 |
| Variable costs per day | $ 24,906 |

Appendix Table 16. Surimi (large) mothership.

| | |
|---|---|
| Length | 460 feet |
| Crew size | 300 |
| **Fixed Costs** | |
| Vessel value | $45,000,000 |
| Interest rate | 10.00% |
| Length of loan (years) | 15 |
| Capital costs | $5,916,320 |
| Hull insurance rate | 6.00% |
| Hull insurance cost | $2,700,000 |
| P & I rate/crewman | 8,000 |
| P & I cost | $2,400,000 |
| Overhead | 540,000 |
| Total annual fixed cost | $11,556,320 |
| **Variable Costs** (Catch independent) | |
| Fuel rate/Oper. day (gl) | 4,400 |
| Fuel | $ 1,056,000 |
| Groceries | 1,350,000 |
| Production supplies | 70,000 |
| Repair & maintenance | 800,000 |
| Crew transportation | 540,000 |
| Crew salaries | $12,000,000 |
| Total variable costs | $15,816,000 |
| Variable costs per day | $ 59,693 |



# THE FOUNDATION

The Fisheries Management Foundation was formed in 1985 to support fisheries scientists and managers working to develop innovative solutions to the problems of fisheries management. The Foundation's Board of Managers is composed of recognized experts in fisheries management: Dr. D.L. ("Lee") Alverson, former Director of Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Professor Don E. Bevan, Professor Emeritus and former Dean of Fisheries of the University of Washington, and Professor James A. Crutchfield, Professor Emeritus, Department of Economics of the University of Washington. The initial funding for the Foundation was provided in 1985 by Dr. Keith B. Jefferts and Dr. Lynn B. Squires. The Board will review proposals of fisheries scientists, researchers, and managers in light of the Foundation's broad goals.

## THE CHALLENGE

The Foundation's goals are:

- Harvest levels consistent with long-term economic biological productivity of marine and aquatic resources.
- Optimum economic return from the nation's publicly-owned marine and aquatic resources.
- Production of top quality seafood and aquatic products.
- Education of the general public regarding fisheries issues.

## THE SEARCH

To promote the gathering and dissemination of reliable, timely information, the Foundation provides grants for a wide range of projects. These grants are designed to allow scientists, researchers, and managers to work and teach unburdened by other commitments in an environment free from the influence of institutional policies or political pressures. The Foundation considers proposals involving all aspects of fisheries management: biological, sociological, economic, educational, political, technological, and environmental projects to improve the accuracy, availability, and timeliness of fishery data are particularly solicited.

Grant selections are made by the Board of Managers. Proposals are evaluated in terms of conceptual soundness, contribution to improved fishery management, experience and training of the applicant, and adequacy of the proposed budget. The Board may from time to time request outside review of the proposals by qualified experts. The National Science Foundation format for research proposals should be followed.

Inquiries concerning the Foundation and its program should be directed to Fisheries Management Foundation, 2445 Perkins Lane West, Seattle, Washington 98199.

# FISHERIES RESEARCH INSTITUTE

Founded in 1947, the Fisheries Research Institute (FRI) joined with the School of Fisheries in 1958 to become its primary research unit. Research staff and activities steadily enlarged over the years, and the diversity of sponsored research projects has greatly increased since the initial years of exclusive emphasis on salmon problems in Alaska.

FRI has evolved into an institute dedicated to developing, administering, and conducting the School of Fisheries research program in the area of Fisheries Science and Management. The objectives of this program are threefold. First, the program provides relevant research and training opportunities for graduate students. Since fisheries science is a rapidly developing science, it is impossible for faculty to teach and train effectively unless they are deeply involved in that development. Second, the research program exists to advance the state of knowledge, the fundamental understanding, in the field of fisheries science and management. Third, since fisheries is an applied science, the research program must explore methods of applying our understanding to public needs. In this context, FRI, and the University, play a unique role as a link between basic fisheries science, management, and resource user groups. This third role is carried out through contract and grant research, direct participation of FRI faculty, staff, and students in the management process, and the use of FRI as a forum for the development of public fisheries science and management policy.

Fisheries is a broad science, drawing on a large variety of disciplines. Its roots are in the basic biological sciences (icthyology, physiology, behavior, ecology, genetics), and encompasses the physical sciences (limnology and oceanography), mathematics (population dynamics and statistics), social sciences (economics, sociology, public policy), and engineering (hydroacoustics, fishing gear technology).

Fisheries science is also oriented toward solving problems. The FRI program attempts to address these problems in a comprehensive way by conducting individual research efforts in the basic areas and, in addition, developing large multidisciplinary research programs around specific themes or problem areas such as the Alaska salmon fishery. These programs are team efforts that require the active participation of more scientists than can be justified by an academic program alone. These programatic research efforts must have longevity to be of real use to the advancement of fisheries science and the link to managers and users; FRI provides this continuity by employing research faculty and staff and housing postdoctoral fellows and visiting scientists drawn from around the world.

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# Marine Fishery Regulation in the U.S. and the Role of Economic Analysis

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## INTRODUCTION

This paper is intended to provide a broad overview of economics applied to fisheries management. It begins with one of the fundamental issues: "Why regulate fisheries?" The first section summarizes the standard rationale for regulating fisheries and describes a lingering controversy over private ownership versus public regulation. Section 2 reviews the standard critiques of conventional regulations and recommendations for efficient fishery management. Section 3 is devoted to economic aspects of allocating fish and fishing rights. In the final section, I offer some observations on the role of economics and economists in fishery management.

My perspective is derived from involvement in marine fisheries management on the Pacific coast. That includes experience in developing management plans for coastal pelagic species (anchovy, mackerel, and squid), reviewing plans and periodic regulatory proposals for groundfish and salmon fisheries, research and consultations on limited access systems, and a recent study of the developing U.S. groundfish fishery off Alaska. The appropriate content and role of analysis depends upon specific issues, contexts, and policy objectives. These clearly differ among regions and fisheries. I will be interested to learn during this workshop whether the Pacific coast experience is relevant to fishery management in the Gulf and southeast regions.

## WHY REGULATE OCEAN FISHERIES?

The earliest and perhaps most important contribution of economics to fisheries regulation was the development of a coherent rationale for government intervention in the fisheries. That rationale rests on a theory of optimum harvest combined with the dynamics of open access competition. The economically efficient fishery would expand until the marginal cost of additional fishing effort equals the marginal revenue from additional catch. Achieving this would generate a maximum rental income to a manager or owner of the fish stock. The early papers of H. Scott Gordon (1954), Anthony Scott (1955) and James Crutchfield (1956), established that the unregulated fishery will apply more fishing effort than needed to achieve the economic optimum, and that over-investment will occur in fishing capacity, and often in fish processing capacity as well. Without a fishstock manager (private owner or public authority), fishermen compete for fish by expanding capacity until marginal cost of fishing equals average revenue. If costs of fishing effort and the price of fish are constant, this competitive equilibrium yields no resource rents.[1]

Moreover, there is ample experience and documentation showing that commercial fishing fleets in practice do tend to deplete fish stocks and to overcapitalize. The more valuable fish, such as Pacific halibut, salmon, roe-bearing herring, attract the most fishing activity, are potentially the most endangered by unregulated fishing, and have the most highly overcapitalized fisheries.

Overfishing of common property fish stocks is not due to the perfidy and greed of fishermen. Also, it is not lack of foresight (or a high time rate of discount) that accounts for the lack of husbandry among fishermen. It is the absence of private or group ownership, and the concomitant lack of individual opportunity to reap financial gain from stock conservation and enhancement. It is a consequence of vigorous competition in an industry dependent upon an un-owned, depletable resource. Some economists blame overfishing on the absence of exclusive property rights in fishstocks. Lacking private rights to the fish stock, courts of law do not defend individual claims to the economic returns from investments in marine fish, and individuals cannot expect to reap future gains from individual conservation actions. Without price rationing of fish *in situ* through private property rights, markets fail to achieve economic efficiency, and the problem with fisheries is diagnosed as a "market failure."

The theoretical expectations of poor conservation and inefficient production under open access are supported by empirical evidence. A variety of research papers have shown that restricted access to marine fish resources leads to better conservation and greater economic returns. Acheson's (1975) work on Maine lobster fisheries shows the average size of lobsters tend to be larger where "harbor gangs" effectively excluded outsiders. This suggests that yield-per-recruit is increased through lowered fishing mortality in sections of the fishery with a sort of illicit limited entry. Agnello and Donnelley (1975) find statistical evidence that labor productivity in the oyster industry is higher in states with private leasing than in states with open access to oyster beds. Townsend (1985) reaches similar conclusions regarding Maine's soft-shell clam fishery. Coastal towns with restrictive local ordinances enjoyed both higher yield-per-recruit and higher yield per unit effort. These studies depend upon the co-existence of restrictive and nonrestrictive regulatory regimes, which exist chiefly in coastal and inland waters of north America. Since they occur mainly outside of the narrow coastal zone, marine fisheries generate little comparative data of this sort to show that limiting harvest rights yields more efficient harvests.

The case for government regulation of recreational fishing follows a logic similar to that for commercial fishing (McConnell and Sutinen, 1979). Recreational harvests in the marine environment tend to be smaller than commercial counterparts in most circumstances. But the common property problem is essentially identical, and the consequences for fish stock depletion and loss of economic value can be severe when sport fishing takes a substantial fraction of the stock annually.

One solution to the common property problem is, of course, to establish exclusive and enforceable private property rights to the fish stock. Anthony Scott's (1955) "sole owner" would, like the owner of private livestock, have incentives to achieve economically efficient production. The private owner would have a secure right to receive the full benefits of conservation and enhancement efforts, to exclude others from taking those benefits, and to sell or lease his or her rights for a price or rent agreed to in voluntary transactions. Investment in fishstocks by private owners would expand until marginal rates of return equal the relevant interest rates. In theory everyone, producer and consumer alike, would be better off if private property rights were assigned to fish stock owners who then conduct efficient harvest programs.

While private ownership is practical for some marine organisms, the legal basis for exclusive, private holdings outside of tidal waters is absent, and the division of the marine ecosystem into private holdings might be impractical or unenforceable. James Crutchfield (1956), for example, claimed that fish stocks are incapable of ownership. This highlights two related issues that are still being debated: (1) whether it is feasible to divide up fish stocks into private property shares, and (2) whether it is useful to replace government regulation with private property and markets. Most fishery management personnel do not seriously consider establishment of exclusive private property as an alternative to government regulation. This presumption for regulation is fostered by legislation like the Magnuson Fisheries Conservation and Management Act, and by the obvious problems associated with open access fishing.

Private property rights have never been given a fair trial in marine fisheries. The development of property rights in fishstocks, according to A. Scott (1988), was severely retarded in English law by the Magna Carta. Canadian and U.S. law followed the English tradition. Where exclusive harvest rights are exercised in fisheries (primarily in freshwater ponds, streams, and tidal shellfish beds), they are apparently a useful mechanism for achieving conservation and economic efficiency. But private leaseholds for sedentary, intertidal resources, and ownership of fish stocks appurtenant to riparian property do not provide realistic examples for marine fisheries. In the ocean, harvest of one species at a given time and place frequently affects other species, harvested by other fisheries or by the same fishermen at different times and places. Also, fish harvests affect populations of protected marine mammals and some endangered species. To the extent the public is entitled to protection from these spillover effects, private ownership in marine fish stocks would not obviate the demand for regulating fishing activity.[2]

Nevertheless, some analysts of natural resource regulation reject the presumption that government regulation is an improvement on private ownership (e.g. T. Anderson, Libecap, and Stroup and Baden). The arguments hinge on two salient points. First, although private markets in resources are imperfect, due to mobility and complexity of the biological stocks and externalities, government regulation is not necessarily superior. Self-interests and political influences in agency decision making can cause significant divergences from economically efficient resource use. It is unrealistic to assume that regulators are powerful, effective, and beneficent decision makers, whose actions in the collective interest are accepted and heeded by the regulated.

Management agencies are sometimes "captured" by the industries being regulated, resulting in management for the benefit of those special interests. Also, because personnel in regulatory agencies are not financially rewarded for economic performance of the resource industries, their incentives to devise efficient harvest plans are weak, and they are prone to respond less to economic signals than to politics. This does not impugn the character of agency personnel; it simply extends to the individuals in government service the logic of rational, self-interested behavior. In sum, this view of resource economics quite properly concludes "that the absence of property rights can generate market failure but that incentive structures within government can generate government failure" (T. Anderson, p. 5).

A second concern about government regulation is that it fosters counter-productive "rent-seeking" behavior. Competition for rents available from government regulated fisheries is somewhat like open access competition for fish. Those affected by regulations will expend money and time to sway decisions in their favor and to avoid the consequences of regulations once promulgated. If a shift in quota or area or season timing can increase the competitive edge of one person over another, he or she can be expected to spend time and money to influence the decisions. A self-interested, rational individual would spend on political influence so long as the expected effect on future earnings exceeds the cost of seeking rents through such influence. Fishermen groups may feel a need to hire spokesmen, to retain lawyers, and to set up "research foundations" in an effort to shift potential fishing opportunities and profits to their members. The resources expended in this manner are lost in a zero-sum game among the competing groups.[3]

It is unclear to me whether we should be troubled by the potential for rent-seeking behavior. We do not know whether this source of inefficiency in the fisheries will seriously diminish the value of newly emerging management techniques like individual quota shares. Also, it is unclear to this author that rent-seeking surpasses ideological demagoguery as a motivating force in fishery politics. I will proceed on the assumption that it is feasible to improve government management of fisheries without establishing exclusive private property rights to marine fish stocks.

## REGULATION FOR GREATER EFFICIENCY

Besides providing a coherent explanation for the overfishing problem, economics supports an extensive critique of various regulatory approaches. All economic assessments of fishery regulation (beginning with J. Crutchfield (1961) and continuing through the textbooks of Anderson (1986), and Cunningham, Dunn and Whitmarsh (1985)) conclude that conventional, direct regulation of fishing activity cannot successfully solve the open access problem. Annual quotas, season closures, gear restrictions, fish size limits, and so forth deal simply with symptoms, not the disease. Conventional regulations do not create conditions under which exercise of normal business incentives will lead to optimal fishing capacity.

Conventional fishery regulations, in the face of open access competition, *can* reduce effective fishing effort to achieve target harvests (equal to maximum sustainable yield, or maximum economic yield, or any other criteria). It can be shown that limiting fishing effort through season closures or gear restrictions will attain a target quota by causing an increase in the cost of harvesting. Whether or not it is regulated via quota, the competitive fishery will be in economic equlibrium when average cost per unit harvest equals average revenue—that is, when no prospective profit induces entry of new fishermen or expansion by existing fishermen. With annual quotas, fishing effort cannot expand beyond that necessary to take the quota, but the costs of applying that level of effort is unregulated. Fishing costs will increase as overcapitalized fleets compete for the quota during short fishing seasons.[4] By allowing average cost to equal the price, conventional regulations assure the dissipation of any potential net value.

I hesitate to conclude that conventional regulations are unconditionally worthless, especially when they increase the size of fish stocks, improve the average size of the fish, protect endangered species, and reduce the chances of recruitment failure. While conventional regulations seldom produce any worthwhile efficiencies in fish harvesting, processing and distribution, they may improve overall product value by maintaining a desireable mix of fish size and species and they may raise consumer surplus in final product markets by maintaining large total annual harvests. In the absence of more effective regulations, it seems prudent to continue adjusting conventional regulations to increase the value of a given quantity of harvest.

As a guide to the importance of seeking efficiency in harvesting, economists can estimate the size of the potential economic rents that are up for grabs. For example, I recently estimated the potential rents for two multispecies groundfish fisheries (Huppert and Squires, and Huppert, 1988). Both assessments were based upon assumed biological catch limits, and upon average fishing costs and fish prices. Computations used standard linear programming methods. On the Pacific coast, the groundfish trawl fishery could yield about $12 million in net revenue. Similarly, in the Bering Sea and Aleutians Islands area an optimal fleet of factory trawlers and motherships would generate around $124 million annually. In both cases the profit is around 15% of the gross revenue. Both represent gains from efficiently harvesting an arbitrary quantity rather than the maximum net value associated with optimizing both harvest efficiency and total yield.

The principal types of economic regulation that could generate these rents are (1) taxes and fees, and (2) the various forms of limited access. Using these regulatory approaches, one can seek an economic optimum yield by simultaneously adjusting both harvest quantities and harvesting costs. Or, taking biological yield guidelines as target catch levels, one could seek only to minimize fishing costs. Generally, the theory of taxes and fees for optimum fishing deals with optimum yield. Facing fish landings taxes (or royalties) equal to the true social net value of fish *in situ*, the competitive fishing fleet would adjust to the appropriate overall yield. Limited access, on the other hand, is concerned primarily with controlling excess fishing capacity and costs.

Taxes and fees have long been a favorite topic for economic theorists of environmental regulation. It can be shown with mathematical rigor that the proper taxes and fees applied to the inputs and outputs of harvesting firms can mimic the costs that would be imposed through ideal markets in fish resources. These fees bring private costs of profit-seeking harvesters into line with true social costs of fishing, and no further direct regulation is needed (Clark). Several practical and legal concerns militate against the use of taxes and fees. An economic argument against taxes is that fees will impoverish fishermen in the short run, because any increase in operating costs would cause average returns to drop below average costs (e.g. Cunningham, et al., p.163). Following the argument of M. Weitzman (1974), fisherman would receive lower incomes even in the long run, under any form of centralized management that transfers rental value of the resource out of the fishery. Thus management via taxes would generally be unattractive to the most influential groups in the fishery. Given the forces marshalled against taxes, I will go on to other options.

Limited access is basically of two types: license limitation and individual quota shares. These measures constructively address the open access problem, but they do not fully remove the problems associated with lack of property rights in fish. Myriad license limitation programs in North American, Australia, and New Zealand are well documented in the literature. (See Rettig and Ginter, 1981; Sturgess and Meany, 1982; Fraser, 1979; Rettig, 1984; and Mollett, 1986.) Most economics treatises on license limitation programs now list a series of shortcomings. A license to fish, without quantitative limits on harvests, does not alter the basic competition for fish among fishermen. Hence, minimization of fishing costs will not happen under license limitation. This shortcoming is especially pronounced in fisheries that have excessive numbers of fishing vessels at the outset of the limitation program.

Individual fishermen quotas are widely recognized as perhaps the most promising regulatory method for improved economic efficiency. They have been implemented recently in New Zealand's groundfish fishery (named individual tradeable quotas, ITQs) and in Australia's southern bluefin tuna fishery, and a similar system (enterprise quotas) is operating in Canada's north Atlantic offshore groundfish fishery. The key to this method is that it comes close to reproducing the conditions of a property right. When quota shares trade in open markets, the share prices approximate the scarcity value of fish, even though the share does not convert the fish stock into property.

Proponents of the technique (New Zealand Ministry of Fisheries personnel being among the most zealous spokesmen) point out the myriad dimensions in which fishermen can optimize harvest operations under ITQ's. Fishermen will be able to change fisheries through buying and selling rights to alternative species; they will be able to use the proceeds from selling their ITQ's to finance retirement; and the government will alter the annual level of harvests through buying and selling quotas. Economic efficiency of harvesting will be substantially improved as the quotas migrate to the most efficient fishermen and fishing firms accumulate shares to achieve optimum size operations.

Possible drawbacks to ITQ's include the difficulty that government enforcement officers may have in monitoring harvests and in detecting infractions. Without a credible enforcement effort, the similarity to private property status for share quotas will evaporate. (See F.G.Peacock and D.A. MacFarlane, 1986). Where fishing is multispecies, the ITQ may exacerbate the incentives for discarding by-catch of species for which shares are not immediately available. The New Zealand system has attempted to deal with this aspect, but some observers (e.g. Copes) are not convinced that the problem is solved.

In the United States, regulations to improve efficiency in fish harvesting are not widely adopted. Where adopted, their effectiveness is not demonstrably great. The most prevalent "economic" regulation is license limitation, which has been implemented in a myriad Pacific coast fisheries. British Columbia's salmon license program, initiated in 1969, is the oldest and most closely analyzed system. On the U.S. Pacific coast, all the non-Indian, commercial ocean salmon fisheries have been under license limitation since 1979. California has imposed license limitations on the roe-herring fishery, the abalone fishery, and the gill net fisheries (Huppert, 1986). Alaska has a most extensive system of license limitation for salmon fisheries (Schelle and Muse).

The available retrospective economic assessments of these license limitation systems (Fraser, 1979; Pearse and Wilen, 1979; Huppert, 1982; and Schelle and Muse, 1986) have found conflicting evidence of increased economic efficiency. Fraser (p.760) and Pearse and Wilen (p.768) reported that continued investment in the fishing fleet under the licensing program threatens the emergence of any economic rent. Huppert found some evidence of economic profits under California's nontransferable license system for roe-herring. But that evidence was a short-run event, as roe prices subsequently declined and the state expanded the number of permits. Schelle and Muse interpret the sustained, high prices for salmon fishing permits in Alaska to be indicators of scarcity value. This value would not exist unless expected discounted future profits in the fishery were positive (see Karpoff, 1984). Overall, the economic assessments of license limitation in the Pacific fisheries tend to be lukewarm regarding the potential for efficiency and rent creation.

## ALLOCATION OF FISHERY RESOURCES

Because allocation of fishery resources is an increasingly contentious topic, it is important to use the term "allocation" carefully. Economists are accustomed to "resource allocation" as a topic dealing with the allocation of various inputs (labor, capital, land, intermediate goods) among industries or among firms. In this sense, to optimize a fishing fleet or the amount of fishing applied to a given stock is an exercise in resource allocation. The economics of resource allocation deals mainly with efficiency. On the other hand, the discussion of allocation in fishery management circles concerns the distribution of fishing rights or fish among individuals or groups of individuals by a public authority. This version of "allocation" deals more with assignments of property and resource ownership, and concerns shifts in assets or opportunities among distinct groups of people, not among industries. Choice of allocations can be based on either efficiency or equity. Through the remainder of this section, I will use the term in this latter meaning.

Most conventional fishery regulations under open access involve no explicit allocations, as each fisherman has a co-equal right to fish. Conventional regulations do *cause* allocations, however, especially when a particular geographic area of the fishery is closed, or a particular gear type is prohibited. In California, for example, bottom trawl nets are prohibited within three miles of shore, purse seine nets may not operate in Santa Monica Bay, and commercial abalone divers may not fish in waters north of Monterey. In the anchovy fishery management plan, specific seasons were closed to the commercial purse seine fishery in order to reduce "conflicts" with recreational fishermen. In each case, the area or fish or season prohibited to one group of fishermen is implicitly allocated to another group.

Explicit allocations of fishing rights among fishermen associated with various gear groups, or between recreational and commercial fishermen are also commonly adopted along with conventional regulations. The Pacific Fishery Management Council (PFMC) allocates the annual harvest guideline for sablefish between otter trawl vessels and fixed gear (longline and pots). In California, marlin, kelp bass, and striped bass have been declared unconditionally for recreational use only. PFMC's salmon management plan allocates the coho and chinook harvests between recreational and commercial fisheries on the basis of a sliding scale. North of Cape Falcon, for example, as the coho salmon quota increases from zero, the recreational fishery allocation starts at 70 percent but falls at a rate of 10 percent for each increase of 300 thousand coho salmon quota.

Initial allocations of fishing rights or licenses in a limited entry system raise many difficult issues. The Alaska salmon license limitation law, for example, required a reduction in number of permits below the total number of fishermen with past experience in the fishery (Schelle and Muse, 1986). Eligibility for the limited number of permits was to be based upon past participation and economic dependency. The complicated points system developed to implement the legislative intent fostered many lawsuits which have continued to trouble the Commercial Fisheries Entry Commission for two decades. Most license limitation systems have avoided much travail by issuing permits to every fishermen with a shred of claim upon the fishery. Doing this to avoid tough allocation issues, however, removes any possibility that license limitation can yield any quick returns through reduced capacity and fishing costs.

Economic efficiency criteria can be applied to allocations via the *compensation principle*. The compensation principle states that a change is beneficial overall if the winners can compensate the losers. This is, of course, the principle which stands behind standard benefit-cost analyses. Applied to allocations of fish, the crucial question would be whether the fish (or fishing right) is allocated to the group which values it most, or to the group that produces fish most efficiently.

In evaluating a proposed change in the recreational-commercial salmon allocation, PFMC economists displayed the estimated net economic value changes associated with alternative allocation formulas (PFMC, 1988). Except when salmon quotas are exceptionally low, the new proposed formula would cause a positive net change in value. The salmon allocation analysis also estimated personal income impacts based upon county input-output models. Personal income generated in coastal counties was reckoned to be larger under the new allocation formula as well, except at very low quota levels. Unfortunately for proponents of the revised allocation, the projected harvest quotas for 1988 fell into the low end of the range, leading to expected reductions in both net economic value and community personal income. The Secretary of Commerce's failure to approve the new allocation formula was based in part on the demonstration of its negative economic effects.

A variety of empirical models can be used to quantify the extent of economic value or income redistributions caused by implicit or explicit allocations. In his analysis of the Atlantic coast menhaden fishery regulation, for example, V. Blomo (1987) used a bioeconomic model to show that a geographical redistribution of income may accompany conservation measures designed to increase yield-per-recruit. Reduced harvest of recruits can yield an overall increase in catch and value of catch, while shifting the menhaden fishery from autumn to summer and from south to north. The South Carolina fishery would lose an estimated $4.9 million in profits over a five year period, while the Atlantic fishery as a whole would enjoy an increase in profits of $10 million.

Decisions regarding allocations are frequently not concerned with efficiency of the resulting distribution of rights or fish, but with the equity or fairness in the distribution of economic opportunities. Thus, while allocations do have efficiency effects, these are generally of secondary interest. For economic analysis to be helpful, we need a concept of economic equity that can be applied as coherently and reliably as the efficiency criteria. In the absence of a standard for equitable allocation (or, in the menhaden case, of income redistribution), economic information on regulatory impacts will highlight the degree of economic conflict between the groups without endorsing, or even outlining, a course of action.

## ROLE OF ECONOMICS IN U.S. FISHERY REGULATIONS

Fishery regulations under the Magnuson Fisheries Management and Conservation Act (MFCMA) are deimplementation by the U.S. Secretary of Commerce. The route from initial planning to publication of regulations varies from case to case, but it includes at least a formal Council "scoping session," review by scientific committees and industry advisors, formal public hearings and review of draft documents, preparation of Environmental Impact Assessments, economic impact reviews, and Secretarial review. As is typical of U.S. regulatory processes, the federal management system affords many opportunities for interested parties to enunciate specific objectives, to make suggestions and criticisms, and to influence the outcomes.

Economics is a useful tool in developing fishery regulations, because it deals coherently with efficiency in harvests and predicts shifts in distribution of income. Besides being useful, economic analysis has a formal place in the process. Economic factors are part of the "optimum yield" objective (MFCMA, Sec 303(b)6). The National Standards (MFCMA, Sec 301(a)) include "efficiency in utilization of fishery resources" as one criteria for management plans, and Executive Order 12291 requires evaluation of economic impacts of regulations. These provisions of the law and administrative procedure place a responsibility upon the Regional Fishery Management Councils to consider and document economic consequences of their proposed regulations. The Secretary of Commerce may approve or disapprove regulations based on the prospective economic effects.

In complex, participatory decision making, however, it is typical that objectives are diverse and frequently ambiguous. Policy analysts, such as Charles Lindblom (1959), note that economics is but one approach to problem solving and that non-economic considerations prevail. Economic theories lean heavily on optimizing calculations that require well specified objectives and constraints. Thus, policy analysts view economics as ill designed to handle issues in democratic decision making where the dividing line between ends and means is often hazy. From this viewpoint, the use of economic benefit-cost analysis to solve public resource management problems may not result in good decisions, because it substitutes narrow efficiency criteria for the more practical goal of finding effective consensus through adjustments among competing objectives and values.

Many of us have experienced a sort of professional disorientation when confronted with the disparity between decision making and professional advisory roles. When the PFMC voted to approve a specific anchovy quota formula, for example, it chose from a set of options that we on the plan development team had devised and reviewed. The harvest quota options differed qualitatively, but not grossly, from a formula that I had calculated as an optimum stochastic feedback control strategy (see Huppert, 1981). I did not quibble with the Council's choice, because I knew that several other considerations (e.g. the need for forage fish, conflicts between commercial purse seine fleet and live-bait fleet, etc.) had to be accommodated. Once the decision was reached, however, we were required as a matter of bureaucratic process to document why the Council's decision was the optimal one. It was not clear what objectives were sought via what management actions; but it was clear that different council members voted for different reasons. Thus an ambiguous intellectual exercise was created by imposing an economic-bureaucratic criterion upon an essentially political process.

Thus, the actual, as opposed to formal, role of economic analysis is often unclear. Because decisions are essentially political, not strictly economic or technocratic, it is rarely obvious when specific features of a regulatory package stem from economic considerations. Economists have frequently wrestled with the conflicting roles they play as technical analysts/advisors and as decision makers or seekers of consensus. Several recent papers reflect economists' self-evaluation of their roles (Schultze (1982), Leman and Nelson (1981), Brandl (1985), and Nelson (1987)). These writers emphasize the need for economists to avoid becoming political hacks and to avoid using their economics training simply to rationalize political decisions. To be successful policy advisors, economists must learn to recognize political costs as well as opportunity costs in devising management advice; they must be as conscious of distributional effects as of efficiency effects; and they must "pay their dues" in resource agencies before achieving the level of cooperation and respect of which we are all clearly deserving.

The redistribution of income that Blomo projected for the menhaden fishery regulation is just the sort of trade-off that politically astute decision makers dislike. While the benefit/cost ratio is positive (i.e. the compensation principle is satisfied), actual compensation of losers is unlikely to occur. If both the potential losers and winners are represented in decision making, approval of the conservation plan may require compensating measures of some sort. A more difficult, but politically more acceptable, principle is that of "no losers." A tremendous amount of effort may be required to assure that a given regulation creates no significant uncompensated losers. I suspect that many otherwise inexplicably complex management measures adopted in fisheries represent practical efforts to avoid creating losers. Associated inefficiencies may represent a "political cost" of public decisions.

Recent experience does not provide copious evidence that economists can effectively influence fishery management decisions. Economics is frequently dismissed as superfluous, or too narrow, or not pertinent to practical decision making requirements. I believe this is incorrect, of course, but I also acknowledge the difficulty of incorporating economic information in management decisions. The vigorous politics of competition for allocations can make efficiency and equity seem unnecessary distractions.

Despite the political character of public decisions, however, economics can play an essential role in the development and evaluation of fishery regulations. Decision makers cannot evaluate alternatives without analysis of consequences; and economic consequences are clearly important. The existence of non-economic objectives and values makes it doubly important that government regulations receive thorough economic review. Non-specialists too frequently exhibit unwarranted confidence in their understanding of economics. How many times have I heard that we need not worry about the economics of fishing because "the market will take care of it?" Special interest groups are quick to portray their narrow economic interests as equivalent to the public interest. A thorough training in economics prepares one to view resource allocation and income distribution in the broad perspective that is pertinent to public resource management.

Charles Schultze (p.66) admonishes the economic advisor not to respond to the politics of policy decisions by watering down economics advice with political judgments. This is certainly good advice to fishery economists. Even though the fishery councils are political, and biological considerations crowd the technical agenda, economists have a professional duty to develop and state conclusions regarding the efficiency and income distributional consequences of decisions. The economics research agenda for fishery regulations has been thoroughly prospected by the theorists of yesterday, but the field is still wide open for the dedicated practitioner.

## NOTES

[1] The complete exhaustion of all rent occurs if (1) costs of fishing are proportional to fishing effort (an aggregate input) and (2) competition leads the fleet to a zero-profit equilibrium. The mere statement of these conditions suggest two good reasons for rents not to be exhausted even under open access. First, there frequently appears to be an upward-sloping supply curve of labor in fishing (or an uneven distribution of talent and skill), so that fishing effort is supplied at increasing marginal cost. The industry equilibrium will occur where marginal cost equals price, leaving potentially hefty intra-marginal rents to better fishermen. Further, M. Weitzman (1974) showed that, with a rising supply of inputs, the variable factors will receive greater average incomes with free access than under a private property equilibrium in which rentiers own the fish stock and hire variable inputs. Johnson and Libecap (1982) note that heterogeneity among Texas shrimping firms leads to rising marginal costs.

A second reason, noted by Crutchfield (1956), is that with monopsonistic waterfront fish markets, the tendency to overfish might be substantially attenuated, as the dominant buyers force prices down to the minimum average production cost. This argument suggests that actions by firms with broader interests than individual fishermen could "manage" the fish stocks. There are many ways to organize for increased net economic returns from fishing. Fisherman cooperatives, labor unions, and marketing organizations are some alternatives to monopsonistic buyers and sole owners.

[2] V.K. Smith comments that creation of exclusive rights would involve destruction of pre-existing entitlements to harvest fish. Thus, rights facilitating private market transactions cannot be created in a vacuum.

[3] I speculate that many resource managers wishing to deflect pressures by user groups do so by making the users feel that they cannot gain by influencing the decisions. One useful tactic might be for the manager to disavow any interest in the economic outcomes of resource decisions, thus creating the impression that no user groups will have decisions influenced to their advantage by lobbying activity. If they believe this, interest groups would stick

to "racing for fish" and not devote significant effort to influencing decisions. One form of this tactic would involve the creation of a non-economic resource ethic. Managers could, cynically or fervently, make repeated and consistent public declarations that only biological conservation and the "health of the resource" matter in making decisions. In this ideological milieu, interest groups could attempt to influence decisions by providing alternative interpretations of the biological basis for quotas and allocations.

[4] The Pacific halibut longline fishery continues to be the classic example of this phenomenon. Between 1980 and 1986, the amount of fishing effort increased by 183 percent in response to price increases and productivity-increasing technical innovations (D. McCaughran, 1987). To maintain annual quotas, fishing seasons have been reduced from 20 days to two and one-half days in important regions. The concentration of fish catch in shortperiods prevents fish from entering the fresh market where prices would be higher than in the frozen fish market. Having more freetime and experiencing strong demand from the Japanese market, the halibut longline vessels have increasingly switched to sablefish fishing. So, during 1975 to 1986 the number of sablefish longliners increased by a more than seven-fold. Even though sablefish annual quotas have been increased in recent years, the open season in East Yakutat, for example, has dwindled from 180 days in 1984 to 9 days in 1987 (NPFMC, 1987).

## REFERENCES

Acheson, James M. "The Lobster Fiefs: Economic and Ecological Effects of Territoriality in the Maine Lobster Industry". *Human Ecology* 3(1975): 183-207.

Agnello, Richard J. and Lawrence P. Donnelley. "Property Rights and Efficiency in the Oyster Industry". *J. Law and Economics* 18(1975): 621-34.

Anderson, Lee G. *Economics Analysis for Fisheries Management Plans.* Ann Arbor Science Press. (1981).

Anderson, Lee G. 1986. *The Economics of Fisheries Management 2nd Edition.* The Johns Hopkins University Press. Baltimore.

Anderson, Terry L. *Water Rights, Scarce Resource Allocation, Bureaucracy, and the Environment.* Pacific Institute for Public Policy Research, San Francisco.

Blomo, Vito J. "Distribution of Economic Impacts from Proposed Conservation Measures in the U.S. Atlantic Menhaden Fishery". *Fisheries Research* 5(1987): 23-38.

Brandl, John E. "Distilling Frenzy from Academic Scribbling: How Economics Influences Politicians." *J. Policy Analysis and Management* 4(3,1985): 344-353.

Clark, Colin W. "Towards a Predictive Model for the Economic Regulation of Commercial Fisheries". *J. Fisheries Research Board of Canada* 37(1980): 1111-1129.

Copes, Parsival. 1986. "A critical review of the individual quota as a device in fisheries management". *Land economics.* 62(3):278-291.

Crutchfield, James A. "Common Property Resources and Factor Allocation". *Canadian J. of Econ. and Pol. Sci.* 22(1956): 292-300.

Crutchfield, James. A. "An Economic Evaluation of Alternative Methods of Fishery Regulation." *J. Law and Economics* 4(1961): 131-143.

Cunningham, S., M. Dunn and D. Whitmarsh. *Fisheries Economics: An Introduction.* St. Martins Press, New York, 1985.

Fraser, G. Alex. "Limited Entry: Experience of the British Columbia Salmon Fishery". *J. Fish. Research Board Canada* 36(1979): 754-763.

Huppert, Daniel D. "Economic Analysis for Northern Anchovy Management", In L.G. Anderson (1981): 41-80.

Huppert, D.D., editor. 1987. *Limited access alternatives for the Pacific groundfish fishery.* NOAA Tech. Rep. NMFS 52. U.S. Dept. Commerce, NOAA, Seattle, WA. 45 p.

Huppert, Daniel D. and Melvyn Odemar. "A Review of California's Limited Entry Programs" In Mollet (1986): 310-312.

Huppert, D.D. and D. Squires. 1987. "Potential economic benefits and optimum fleet size in the Pacific coast trawl fleet". *Marine Resource Economics* 3(4): 297-318.

Huppert, Daniel D. "Managing Alaska Groundfish: Current Problems and Management Alternatives" Fisheries Research Institute, University of Washington, #FRI-UW-8805, Seattle, 1988.

Johnson, Ronald N. and Gary D. Libecap. "Contracting Problems and Regulation: The Case of the Fishery". *Amer. Economic. Review* 75(1982): 1005-1022.

Karpoff, Jonathan M. "Insights from the Markets for Limited Entry Permits in Alaska." *J. Fish. Research Board Canada* 41(1984).

Leman, Christopher K. and Robert H. Nelson. "Ten Commandments for Policy Economists". *J. Policy Analysis and Management* 1(1,1981): 97-117.

Libecap, Gary D. *Looking Up the Range: Federal Land Controls and Grazing.* Pacific Institute for Public Policy Research, San Francisco. 1981.

Lindblom, Charles E. "The Science of 'Muddling Through'." *Public Administration Review* 19(2,1959): 79-88.

McConnell, Kenneth E. and Jon G. Sutinen. "Bioeconomic models of Marine Recreational Fishing." *J. Environmental Econ. and Manage.* 63(1,1979): 127-39.

McCaughran, Donald A. "Opinion." *Pacific Fishing Magazine* (November, 1987): 154.

Miles, Edward, Robert Pealy, and Robert Stokes. 1986. *Natural Resource Economics and Policy Application: Essays in Honor of James A. Crutchfield.* University of Washington Press, Seattle.

Mollett, N. 1986. *Fishery access control programs worldwide: proceedings of the workshop on management options for the north Pacific longline fisheries.* Alaska Sea Grant Report No. 86-4. University of Alaska, Fairbanks, Alaska.

Nelson, Robert H. "The Economics Profession and the Making of Public Policy". *J. Econ. Lit.* 25(March, 1987): 49-91.

North Pacific Fishery Management Council. "Discussion Paper: Long-range goals, Objectives, and Techniques for Managing North Pacific Groundfish Fisheries." (Unpublished manuscript dated July 23, 1987).

Pacific Fishery Management Council. "Final Environmental Assessment for a Proposed Emergency Rule Implementing Non-Indian Ocean Salmon Harvest Allocation North of Cape Falcon, Oregon." Portland Oregon (1988).

Peacock, F. Gregory and Dougald A. MacFarlane. "A Review of Quasi-Property Rights in the Herring Purse Seine Fishery of the Scotia-Fundy Region of Canada." In Mollett (1986): 215-230.

Pearse, Peter H. and James E. Wilen. "Impact of Canada's Pacific Salmon Fleet Control Program" *J. Fish. Research Board Canada* 36(1979): 764-769.

Rettig, R. Bruce. "License Limitation in the United States and Canada: An Assessment." *North Amer. J. Fisheries Manage. 4(1984): 231-248.*

*Rettig, R. Bruce and Jay J.C. Ginter. Limited Entry as a Fisheries Management Tool.* University of Washington Press, Seattle. (1981).

Schelle, K. and B. Muse. "Buyback of Fishing Rights in the U.S. and Canada: Implications for Alaska." Paper presented at the Annual Meetings of the American Fisheries Society, Ithaca, New York, 1984.

Schultze, Charles L. *The Politics and Economics of Public Spending.* The Brookings Institution, Washington, D.C. 1968.

Schultze, Charles L. "The Role and Responsibilities of the Economist in Government" *Amer. Economic Review* 72(2,1982): 62-66.

Scott, Anthony. "The Fishery: The Objectives of Sole Ownership." *J. Political Economy* 63(2,1955): 116-124.

Scott, Anthony. "Development of Economic Theory on Fisheries Regulation." *J. Fish. Research Board Canada 36(7,1979):725-41.*

*Scott, Anthony. "Catch Quotas and Shares in the Fishstock." In Miles, Pealy, and Stokes (ed.s): 61-96.*

*Scott, Anthony. "Conceptual Origins of Rights-Based Fishing" Draft paper for presentation to NATO Workshop on the Economic Foundations of Rights Based Fishing, Reykjavik, Iceland. July, 1988.*

*Sturgess, N. H. and T. F. Meany, Eds. Policy and Practice in Fisheries Management.* Department of Primary Industry, Australian Government Publishing Service, 1982.

Townsend, Ralph E. "An Economic Evaluation of Restricted Entry in Maine's Soft-shell Clam Industry". *North Amer. J Fisheries Manage.* 5(1985): 57-64.

Weitzman, Martin L. "Free Access vs Private Ownership as Alernative Systems for Managing Common Property." *Journal of Economic Theory* 8(1974): 225-234.

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# A LIMITED INFORMATION APPROACH FOR DETERMINING CAPITAL STOCK AND INVESTMENT IN A FISHERY[1]

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## ABSTRACT

There have been few empirical studies on the level of capitalization and investment in fisheries because the necessary data are often inadequate. Specifically, data on capital stock and investment in a fishery are not routinely collected and compiled or are limited in scope. In this study, a method is provided for estimating the aggregate capital stock and investment in a fishery utilizing the available information. Data on acquisition and list prices and vessel characteristics for a sample of New England vessels are obtained. The data are then used to estimate an hedonic cost function which specifies the acquisition price as a function of vessel characteristics. The resultant equations are subsequently used, with information on vessel characteristics for all New England vessels, to estimate aggregate capital stock and investment. The results indicate that substantial investment occurred in the otter trawl and scallop dredge fisheries, particularly since the Magnuson Fisheries Conservation and Management Act. Moreover, the results demonstrate that the number and change in the number of vessels are inadequate indicators of the level of capital stock and investment in a fleet comprised of vessels with heterogeneous characteristics.

The common property nature of fisheries is recognized as causing excess capitalization and harvesting capacity (Gordon 1954). The theoretical argument is that since fishermen do not have to pay for the utilization of common property fish stocks, new vessels enter a fishery until net revenue is driven to zero. This common-property feature results in more capital and investment than is economically optimum. Public regulation of fishing industries is usually advocated to redress the excess entry, economic inefficiency, and loss of economic rents in a common property fishery (Scott 1979; Sissenwine and Kirkley 1982).

In essence, overcapitalization and excess investment are perceived to be the reasons for many of the major fisheries problems (Hilborn 1983). Economists argue that management of overcapitalization is necessary to realize the benefits of fisheries (Cunningham et al. 1985). Alternatively, gains from fisheries management require control of overcapitalization and excess investment (Charles 1983a, b).

Clark et al. (1979) and Charles (1983a, b) extended the static theory of optimal fisheries investment as developed by Gordon (1954). They also demonstrated the relationships between investment, capital stock, overexploitation, and fisheries management. They concluded that investment should be more conservative to prevent overexploitation.

The economic literature provides substantial justification for the need to solve the problems of overcapitalization and excess investment. Yet, few empirical studies document the level of capitalization and investment.[4] Moreover, there appears to be no attempt by any U.S. agency to routinely collect and compile statistics on either the stock of capital or the level of investment in U.S. fisheries. Overcapitalization and excess investment, though, continue to be suggested as the reasons for many of the economic problems of fisheries.

Since data are often inadequate, many empirical studies on fisheries consider capital stock and investment in terms of the number of vessels. That is, capital stock and investment in a fishery are tyically measured in terms of number of vessels. In the absence of appropriate information, the number of vessels may be the only basis for examining overcapitalization and excess investment. Alternatively, if a fleet has identical-sized vessels, fixed inputs or vessel characteristics, and

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[4] Tettey et al. (1986) provided an exception, but their analysis is restricted to the shrimp fishery and is based on cost data obtained from boat builders.

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gear, the number of vessels may be used to indicate the stock of capital and investment. However, Kendrick (1961) demonstrated that the total number of operating units, such as the number of plants, is an inadequate measure of capital stock. Also, few fleets have identical-sized vessels, characteristics, or gear. As a consequence, the number of vessels does not provide adequate information to indicate the level of capitalization and investment.

This study presents an approach for estimating the aggregate or industry level of capital stock and investment in a fishery comprised of heterogeneous vessels using available information. Data available include acquisition and list prices for some but not all vessels and boat characteristics for all vessels in a fleet. The approach was developed and used to obtain estimates of capital stock in support of the United States and Canadian maritime boundary dispute. It is viewed as an initial step towards examining the problems of excess capitalization by providing estimates of aggregate capital stock and investment.

## THE DEFINITION AND MEASUREMENT OF CAPITAL AND INVESTMENT

### Capital

The concept of capital has created problems for economists for quite some time. The term has been used in so many different contexts that it is a source of enormous confusion (Hirshleifer 1970). Sloan and Zurcher (1968), in their "Dictionary of Economics", define capital as "One of the major factors of production consisting of property from which an income is derived, expressed in terms of money. Popularly, the term is frequently used interchangeably with capital good. A distinction is sometimes made between money capital, or that part of the capital held in the form of money and bank deposits, and property capital, or that part of the capital held in the form of evidences of ownership such as stocks, bonds, and mortages."

Hirshleifer (1970) presented three meanings of capital: 1) real capital or capital stock, 2) capital value, and 3) liquid capital. Real capital is defined as a collection of capital goods or an aggregate of heterogeneous capital inputs. It is one of the major productive commodities or economic factors of production. Capital value is the net discounted value of expected future income streams associated with a capital good. Liquid capital is the level of current funds available or intended for investment.

In the case of fisheries, real capital or capital stock is the form of capital which should be examined with respect to the problems of overcapitalization and excess harvesting capacity. It is the relevant measure of capital goods used or available for production (National Academy of Sciences 1979). Moreover, capital stock is the concept of capital used to define and measure the services of capital inputs which are required to harvest fish; that is, it is the concept of capital required to define the economic production technology of a fishery. Thus, this study is concerned with the concept of real capital stock.[5]

The measurement of capital stock in a fishery, however, presents several problems. First, capital inputs are usually quite heterogeneous and cannot be easily aggregated without restrictive assumptions about the form of the catch equation or fishermen's behavior. Conceptually, it should be possible to combine all the different types of capital goods by weighting each type by its average compensation (i.e., the rental price). However, information at this level of detail is typically not available. Second, fisheries agencies, particularly in the United States, generally do not collect and compile information necessary to calculate capital stock and investment. Third, in order to compare changes in capital stock over time, the measure of capital stock must be converted to some base period value by deflation.

In empirical economic studies of traditional industries, the common practice is to measure the capital input or stock by converting the purchase or acquisition price or the book values of capital to base period values by the use of a price index (National Academy of Sciences 1979). Varian (1984) noted: "The usual procedure is to measure capital value and then deflate by a price index; in some sense, this should measure the level of capital stock." In this study, the acquisition price is used as the measure of the stock of capital or capital value; the real stock of capital is obtained by dividing the capital value by the producer price index for heavy machinery.

### Investment

The definition and measurement of investment is more straightforward than is the definition and measurement of capital. In simple terms, investment is the exchange of money for some form of property. Although there are several types of investment (Branson 1972), attention is restricted in this study to an examination of net investment ($i_n$) which is defined as the difference between the stock of capital in two periods of time (Baumol 1977). This is the same concept of investment examined by Tettey et al. (1986).

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[5] The market value of capital, acquisition price, and cost of capital are used interchangeably in this study.

Replacement investment is another type of investment. The sum of replacement investment and net investment equals total investment. Replacement investment is measured by multiplying the rate of depreciation times the level of the capital stock. Replacement investment, however, is not estimated in this study since the method and rate of depreciation must be arbitrarily assumed.

## METHOD OF ANALYSIS

### The Hedonic Approach

While the definition and measurement of real capital stock and investment are conceptually straightforward, limited data and heterogeneous capital inputs complicate the measurement of capital stock and investment. In particular, data are usually only available for a small number of vessels which are often similar in their characteristics; these data are inadequate for calculating actual or observed capital stock and investment in a fishery. However, data are available on the acquisition price and characteristics of vessels which permits estimation of the stock of capital by an hedonic approach. In turn, estimates of capital stock from the hedonic approach can be used to estimate net investment in a fishery.

The hedonic approach hypothesizes that the price of a commodity is influenced by its characteristics (Rosen 1974). The hedonic price or characteristics function in market equilibrium reflects both the distribution of marginal rates of substitution over households and the distribution of marginal rates of transformation over firms. In effect, the hedonic hypothesis states that goods may be valued for their attributes and that implicit or hedonic prices exist as a function of the attributes.

Griliches (1971) estimated hedonic cost functions of U.S. automobiles using advertised or list prices and actual transaction prices. Griliches, however, was concerned with explaining quality differentials. Ladd and Martin (1976) examined prices and demands for input characteristics using a Neoclassical input characteristics model. Triplett (1986) estimated quality adjusted price indexes for computers. Thus, there is a history of deriving prices of commodities as a function of their characteristics.

The hedonic approach offers several attractive properties for estimating capital stock in fishing industries. First, the hedonic method incorporates changes in the quality of capital over time (Triplett 1986). This is because changes in quality should be reflected in vessel acquisition prices. The hedonic approach, thus, permits a quality adjusted measure of capital stock to be obtained. In contrast, vessel count ignores changes in the quality of capital. Second, the hedonic approach allows easy aggregation of the heterogeneous capital inputs frequently observed in a fishing fleet because the heterogeneous capital is measured by value rather than physical measures.

In the hedonic approach, cost (C) or input price may be expressed as a function of the associated characteristics of the commodity or input,

$$C = f(CH_1, CH_2, \ldots, CH_n) \ , \tag{1}$$

where C is cost, $CH_i$ is the $i$th characteristic (Braeutigam et al. 1982). The characteristic cost equation can be obtained either from a dual specification or by determining the reduced form equilibrium equation.

### The Dual and Reduced Form

The dual specifies cost as a function of input prices and their characteristics. The partial derivative of the dual cost function with respect to input prices yields the demand for the inputs as a function of prices and input characteristics. The reduced form is obtained by solving structural equations, equations which explain the behavior and interrelations of endogeneous variables, of demand and supply for the endogeneous variable, price, in terms of exogeneous variables and disturbance terms.[6]

In this study, the reduced form is directly specified and estimated for two reasons: First, all of the input price data necessary for estimating a dual are not available. Second, estimation of the structural equations is complicated by the need to use a limited dependent variable method of estimation since demand is a discrete choice, and there are individuals or firms which do not purchase a vessel.

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[6] See Rosen (1974) for additional information on obtaining reduced form equations for hedonic prices.

Rather than attempt to deal with these difficulties which do not appear to have widely accepted solutions, it is assumed that there are underlying structural equations of demand and supply which permit the derivation of the reduced form equation. Moreover, the direct specification and estimation of the reduced form is the more commonly used approach to estimate the value of a commodity as a function of its characteristics (Bockstael et al. 1986). Last, the use of the reduced form should not create a problem since the hedonic function is a joint envelope in characteristic space of demander's bid schedules and sellers offer schedules, and thus, the observed implicit price locus is a reduced form equilibrium vector reflecting both supply and demand influences. As a result, shifts in both market demand and supply are incorporated into the reduced form equilibrium vector.

## The Capital Stock Model

As previously indicated, it is common practice to use the acquisition price as a measure of capital stock. By the hedonic approach, the capital stock or acquisition price of a fishing vessel is postulated to be a function of several vessel characteristics. The following general specification is considered:

$$C = f(LN, CS, YEAR, FI, AGE, DNO, HPWR, GRT), \quad (2)$$

where C is the list or advertised price or the acquisition price of a vessel, LN is length, CS is hull type (1 = steel, 0 = other), FI is fishery or gear type,[7] AGE is age of vessel, DNO is a dummy variable for new and used vessels (DNO = 1 for new and 0 for used), HPWR is engine horsepower, and GRT is gross registered tonnage. The variable year equals the year of the observation. It is included to incorporate technological changes over time, such as the introduction of electronics and stern trawling, and structural changes in the industry such as changes in organization of capital and fish markets and changes in public regulation.

## Functional Form

Several functional forms could be specified for Equation (2). Alternatively, generalized Box-Cox (Box and Cox 1962) transformations could be used to determine the functional form. However, the selection of functional form is mostly concerned with obtaining the relationship between the dependent variable and individual independent variables.This study is primarily concerned with estimating the capital stock. Moreover, it may be quite difficult to estimate capital stock from Box-Cox transformations or other functional forms since the conditional expectation is often of a complex form (Smallwood and Blaylock 1986). Also, Dadkhah (1984) noted that predictions based upon some transformations and functional forms result in biased predictions and asymmetric confidence intervals.

Since this study is primarily concerned with estimating capital stock and investment rather than estimating the implicit prices for characteristics, a linear functional form is proposed for Equation (2). The capital stock equation is specified as a second-order polynominal in order to provide an approximation to an unknown, underlying hedonic function. This is equivalent to specifying a generalized quadratic flexible functional form and imposing zero valued restrictions on the cross product coefficients or interaction terms (Lau 1978). Flexible functional forms are widely used in economic studies concerned with determining the underlying economic structure because they impose very little structure on the economic equations of concern (Blackorby et al. 1978).

## Postulated Relations

The postulated relations between cost and each of the explanatory variables is as follows: 1) the coefficients for the first order terms of vessel tonnage, length, and engine horsepower should be positive since costs should increase as the size characteristics increase; 2) the coefficient for steel-hulled vessels should be positive since steel vessels are generally more expensive than wood or fiberglass vessels; 3) the dummy variable coefficient for new vessels should be positive since new vessels tend to cost more because they are newer and usually incorporate more recent technological advances; 4) the second-order coefficients for the size characteristics are expected to be negative since cost is believed to increase at a decreasing rate in response to increases in the size of a vessel.

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[7] Gear type is an integer valued variable set equal to the gear codes used by the Northeast Fisheries Center. This may influence the results similarly to the use of nonbinary dummy variables (Kmenta 1971). The use of this variable implies that the cost difference between gear types is equal to a scalar multiple of the lowest integer valued gear code. Thus, statistical rejection of cost differences due to gear type is actually a rejection of differences not being equal to scalar multiples. However, the large number of gear codes prohibits their separate treatment.

## THE DATA

Data used to estimate the capital stock equation were obtained from three sources: First, information on vessel acquisition price and associated characteristics were obtained for 164 new vessels from the Northeast Regional Office of the National Marine Fisheries Service.[8] Second, data on list prices and vessel characteristics for 946 used vessels were obtained from various trade magazines and vessel brokers. Third, detailed vessel and fishery data were obtained from the U.S. Coast Guard master vessel listing and the Northeast Fisheries Center. Data were obtained for the years 1965 through 1981.

The first two sets of data were used to estimate the capital stock equations. The third data set was used to estimate aggregate capital stock and investment in selected New England fisheries using the estimated capital stock equations; that is, vessel characteristics for all of the vessels in the New England fleet were inserted into the estimated capital stock equations to obtain estimates of capital stocks per vessel in a given year. The estimated capital stock per vessel was summed over all vessels in a year to obtain total or aggregate capital stock. Net investment was then calculated as the annual change in total capital stock.

The use of both the list and acquisition prices, however, presents a problem. The list price reflects the supply price or the price at which a vessel is offered for sale. The acquisition price reflects the price determined by the equilibrium between demand and supply. As a consequence, estimates of capital stock and investment may be in error.

It is not known by how much the acquisition price differs from the list price for used vessels. Thus, the magnitude of the error cannot be calculated. Since the list price is not less than the acquisition price, estimates of capital stock based on Equation (2) are likely upwards biased. Counter to this problem is the argument that by the time a vessel is ready for fishing, required capital modifications or improvements may result in the capital stock being close in value to the list price.

There are no completely satisfactory economic justifications for using both the list and acquisition prices. Two possible justifications are that Griliches (1971) and others used both prices, and capital improvements or modifications may be nearly equal to the difference between the list and acquisition prices. Another possible justification is the accepted use of cost data obtained from boat builders as in Griffin et al. (1978) which may impose similar problems plus the statistical problem of measurement error. In the remainder of this paper, the term "acquisition price" is used although the estimation and calculation of capital stock and investment are based on both price series.

## EMPIRICAL RESULTS

Equation (2) was estimated by ordinary-least-squares with the dependent variable, the acquisition price, measured in both nominal and real terms; the real price is the nominal price deflated by the producer price index for heavy machinery. As previously stated, deflation is necessary to estimate the real capital stock. The estimated coefficients and statistical results are presented in Tables 1 and 2.

Equation (2), however, was also estimated using data for several groups of years between 1965 and 1981. The reason for considering different time periods was that prior knowledge of New England fisheries suggested that various changes occurred in the fisheries during the selected time periods.[9] Moreover, economic studies of New England fisheries have often been criticized for assuming stable relationships over time or over different cross sectional units. Failure to incorporate changes in the estimated relationship between cost and vessel characteristics over time may result in biased parameter estimates.

Changes which have possible ramifications for the estimated relationships include 1) depressed resource conditions and the presence of foreign fishing between 1965 and 1971; 2) management by the International Commission for Northwest

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[8] Data are confidential and may not be available to other researchers or the general public.

[9] Additional information on possible structural changes in New England fisheries is available in Kirkley et al. (1982), Dewar (1983), Doeringer et al. (1986), and Kirkley (1986).

TABLE 1.—Parameter estimates of hedonic equation for nominal capital stock.

| Years | $N$ | Variables[1] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Constant | GRT | GRT² | HPWR | HPWR² | LN | LN² | YEAR | DNO | FI | CS | AGE | R² |
| 1965–71 | 133 | 13474.9<br>[2](0.30) | 616.45<br>(3.36) | −5.25<br>(5.12) | −201.68<br>(5.58) | 0.51<br>(8.54) | −208.99<br>(0.48) | 11.46<br>(2.89) | −20.0<br>(0.03) | 15692.2<br>(1.89) | −294.2<br>(1.38) | 2315<br>(0.84) | −660<br>(3.35) | 0.93 |
| 1972–75 | 216 | −489183.0<br>(4.72) | −316.47<br>(2.23) | 8.64<br>(10.49) | 52.61<br>(1.03) | −0.13<br>(1.74) | 6330.40<br>(6.10) | −59.33<br>(5.21) | 4722.7<br>(3.40) | 20176.7<br>(2.00) | −290.1<br>(1.10) | 12117<br>(4.95) | −524<br>(2.56) | 0.91 |
| 1976–77 | 164 | −1755240.0<br>(3.58) | 1,335.24<br>(4.30) | 0.72<br>(0.61) | −60.09<br>(0.65) | 0.16<br>(1.65) | 6170.21<br>(4.24) | −56.79<br>(4.04) | 20668.5<br>(3.17) | 24038.5<br>(1.82) | 968.7<br>(1.96) | 12813<br>(3.07) | −749<br>(1.83) | 0.85 |
| 1978–79 | 189 | −3113870.0<br>(2.88) | 673.62<br>(0.72) | −7.87<br>(1.90) | −116 75<br>(0.60) | 0.44<br>(2.06) | 1449.86<br>(0.50) | 44.53<br>(2.02) | 38888.1<br>(2.81) | 2232.4<br>(0.91) | −259.4<br>(0.19) | 13897<br>(1.82) | −6693<br>(8.15) | 0.84 |
| 1980 | 271 | −188637.0<br>(2.22) | 261.24<br>(1.52) | 0.99<br>(0.56) | 224.79<br>(1.65) | −0.05<br>(1.33) | 6059.50<br>(2.09) | −10.82<br>(1.49) | — | 22818.2<br>(1.93) | 1110.8<br>(1.87) | 3969<br>(1.44) | −5867<br>(9.25) | 0.89 |
| 1981 | 137 | −50105.0<br>(1.25) | −4095.43<br>(2.28) | 14.94<br>(2.09) | 198.19<br>(1.60) | 0.21<br>(1.65) | 8208.01<br>(2.06) | −2.72<br>(0.05) | — | 10463.9<br>(1.87) | 75.6<br>(1.39) | 34225<br>(1.74) | −9323<br>(7.20) | 0.78 |
| 1965–81 | 1110 | −528304.0<br>(7.04) | 713.86<br>(2.05) | −0.22<br>(2.15) | −162.83<br>(1.57) | 0.58<br>(5.25) | 4054.12<br>(2.47) | −30.61<br>(2.28) | 5967.9<br>(6.20) | 45970.8<br>(3.59) | 990.8<br>(1.42) | 55730<br>(4.60) | −2217<br>(4.08) | 0.82 |

[1] Variables are defined as follows: 1) GRT and GRT² are gross registered tonnage and its value squared; 2) HPWR and HPWR² are engine horsepower and its value squared; 3) LN and LN² are vessel length and its value squared; 4) YEAR is the year of observation; 5) DNO is a dummy variable for new and used vessels (1 = new, 0 = otherwise); 6) FI is a nonbinary dummy variable for gear type; 7) CS is a dummy variable for hull construction (1 = steel, 0 = otherwise); and 8) AGE is the age of the vessel.

[2] Numbers in parentheses are t-statistics.

TABLE 2.—Parameter estimates of hedonic equation for real capital stock, 1967 = 100.

| Years | $N$ | Variables[1] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Constant | GRT | GRT² | HPWR | HPWR² | LN | LN² | YEAR | DNO | FI | CS | AGE | R² |
| 1965–71 | 133 | 48304.1<br>[2](1.01) | 724.35<br>(3.74) | −6.84<br>(6.33) | −219.74<br>(5.76) | 0.54<br>(8.72) | −388.90<br>(0.85) | 13.86<br>(3.28) | −500.2<br>(0.73) | 18111.3<br>(1.97) | −273.8<br>(1.21) | 2610<br>(0.90) | −653<br>(3.15) | 0.89 |
| 1972–75 | 216 | −81500.3<br>(1.17) | −185.96<br>(1.96) | 5.18<br>(9.37) | 32.62<br>(1.05) | −0.07<br>(1.61) | 4009.60<br>(5.75) | −36.21<br>(4.73) | −117.8<br>(0.13) | 13187.6<br>(1.94) | −213.9<br>(1.21) | 8451<br>(5.15) | −411<br>(3.00) | 0.90 |
| 1976–77 | 164 | −782782.0<br>(2.88) | 738.59<br>(4.28) | 0.47<br>(0.71) | −31.06<br>(0.60) | 0.08<br>(1.18) | 3518.20<br>(4.35) | −32.20<br>(4.13) | 8924.9<br>(2.46) | 12827.3<br>(1.98) | 559.8<br>(2.04) | 11198<br>(3.11) | −422<br>(1.95) | 0.83 |
| 1978–79 | 189 | −1024330.0<br>(2.02) | 331.40<br>(0.75) | −3.76<br>(1.94) | −59.41<br>(0.65) | 0.21<br>(2.16) | 897.93<br>(0.66) | 19.14<br>(1.85) | 12618.4<br>(1.95) | 1074.3<br>(0.09) | −144.4<br>(0.23) | 6882<br>(2.60) | −3147<br>(8.16) | 0.81 |
| 1980 | 271 | −78677.5<br>(2.22) | 108.96<br>(1.52) | 0.42<br>(0.57) | 93.75<br>(1.45) | 0.02<br>(1.33) | 2527.30<br>(2.09) | −4.51<br>(1.49) | — | 9517.2<br>(1.94) | 463.3<br>(1.87) | 1655<br>(1.44) | −2447<br>(9.25) | 0.89 |
| 1981 | 137 | −18958.9<br>(1.25) | −1549.55<br>(2.28) | 5.65<br>(2.09) | 74.99<br>(1.60) | 0.08<br>(1.65) | 3105.60<br>(2.06) | −1.03<br>(0.05) | — | 3959.1<br>(1.87) | 28.6<br>(1.39) | 12949<br>(1.74) | −3527<br>(7.20) | 0.78 |

[1] Variables are defined as follows: 1) GRT and GRT² are gross registered tonnage and its value squared; 2) HPWR and HPWR² are engine horsepower and its value squared; 3) LN and LN² are vessel length and its value squared; 4) YEAR is the year of observation; 5) DNO is a dummy variable for new and used vessels (1 = new, 0 = otherwise); 6) FI is a nonbinary dummy variable for gear type; 7) CS is a dummy variable for hull construction (1 = steel, 0 = otherwise); and 8) AGE is the age of the vessel.

[2] Numbers in parentheses are t-statistics.

Atlantic Fisheries and increased fuel prices between 1972 and 1975; 3) the formulation and implementation of the Fisheries Conservation and Management Act in 1976 and 1977; 4) extremely restrictive regulations in 1978 and 1979; and 5) a long dock strike in New Bedford, frozen harbors, and foreign purchases from American fishermen in 1981. In addition, there was substantial entry of new steel-hulled vessels between 1975 and 1977 and 1979 and 1980.

Chow (1960) tests of the equality of regression equations were conducted to further examine the possibility that the statistical relationships between cost and vessel characteristics changed over time. The Chow test is an F-test of the stability of the coefficients (Maddala 1977). The results of these tests are presented in Table 3.

The results of the tests indicate that the estimated relationships between cost and characteristics were not the same for the selected time periods. Alternatively, the hypothesis of the equality of the regression equations for different periods of time could not be accepted at any reasonable level of significance. However, these results only verify that different models should be estimated for different periods of time. They are not conclusive proof of the selection of the years for a particular group of years. A more accurate determination of the years to be included in each group requires considerably more estimation and hypothesis testing which is beyond the intent of this study.

TABLE 3.—Results of tests for the equality of regression equations.

| Periods tested | F-statistic[2] | Critical values[1] | |
|---|---|---|---|
| | | 0.05 | 0.01 |
| 1965–71<br>1972–75<br>1976–77<br>1978–79<br>1980–81 | 39.38 | $F_{12,1050} = 1.75$ | $F_{12,1050} = 2.18$ |
| 1965–71<br>1972–75 | 8.45 | $F_{12,325} = 1.75$ | $F_{12,325} = 2.18$ |
| 1965–75<br>1976–81 | 20.55 | $F_{12,1086} = 1.75$ | $F_{12,1086} = 2.18$ |
| 1965–75<br>1976–79 | 21.33 | $F_{12,668} = 1.75$ | $F_{12,668} = 2.18$ |
| 1976–77<br>1978–79 | 3.60 | $F_{12,329} = 1.75$ | $F_{12,329} = 2.18$ |
| 1976–77<br>1978–81 | 3.22 | $F_{12,737} = 1.75$ | $F_{12,737} = 2.18$ |
| 1976–79<br>1980–81 | 3.35 | $F_{12,737} = 1.75$ | $F_{12,737} = 2.18$ |
| 1980<br>[3]1981 | 2.76 | $F_{12,384} = 1.75$ | $F_{12,384} = 2.18$ |

[1] F-statistic for denominator degrees of freedom equal to infinity

[2] Restricted residual sum of squares obtained by pooling data over all time periods and estimating Equation (2). Unrestricted residual sum of squares obtained by estimating Equation (2) for each period being examined and then adding the residual sum of squares for each equation.

[3] Residual sum of squares obtained from estimating Equation (2) without the time variable

As indicated by the *t*-statistics in Tables 1 and 2, the age of the vessel, whether or not the vessel is new or used, and the size characteristics appear to be the more statistically significant explanatory variables. These results are consistent with the results of Griffin et al. (1978). The statistically significant negative coefficients for the size characteristics during the years 1972–75 are particularly interesting. These years coincide with the Arab oil embargo when fuel prices increased; expected increases in future operational costs may have deterred new entry. The results also indicate that the value of a vessel declines as it becomes older. The coefficient for hull construction, CS, suggest that steel-hulled vessels are more expensive than are those of other materials such as fiberglass, ferro cement, wood, and aluminum. There does not appear to be a difference in the value of a vessel based on gear type. This may be a result of specification problems with the dummy variable for gear type (see footnote 7).

It is of further interest to examine the elasticities of cost with respect to the vessel characteristics.[10] These are presented in Table 4. As indicated, vessel tonnage, length, and age have the greatest influence on the acquisition price. The elasticity for length is consistent with the manner in which vessels are sold; that is, vessel prices are largely stated in terms of their length.

There are, however, inconsistences in the estimated capital stock equations and elasticities. In

TABLE 4.—Estimated elasticities of cost with respect to vessel characteristics.[1]

| Year | Elasticities | | | |
|---|---|---|---|---|
| | GRT[2] | HPWR | LN | AGE |
| 1965–71 | 0.43 | 0.06 | 2.88 | −0.32 |
| 1972–75 | 0.78 | −0.04 | −0.08 | −0.08 |
| 1976–77 | 1.14 | 0.09 | 0.11 | −0.11 |
| 1978–79 | −0.14 | 0.30 | 2.38 | −0.40 |
| 1980 | 0.16 | 0.30 | 1.43 | −0.30 |
| 1981 | −0.64 | 0.56 | 2.38 | −0.41 |

[1] Elasticities based on nominal estimates and observed mean values of cost and vessel characteristics

[2] GRT is gross registered tonnage; HPWR is engine horsepower; LN is length; AGE is age of vessel.

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[10] Elasticities indicate the percentage change in cost resulting from a 1% change in the value of a characteristic.

particular, not all of the estimated coefficiencts have the desired or expected sign. For example, the coefficient for tonnage in the 1981 estimate is negative and that for the square of tonnage is positive. In contrast, a positive coefficient for tonnage was expected since vessel cost should increase with vessel tonnage, and the coefficient for tonnage squared was expected to be negative because vessel costs are believed to increase at a decreasing rate.

The incorrect signs could be the result of multicollinearity between vessel characteristics. Auxiliary regressions, though, do not indicate severe multicollinearity. The $R^2$ values are $<0.35$. If multicollinearity is a problem, its major effect is on the estimated relationships between cost and individual characteristics, the estimated elasticities, and the previously discussed Chow tests.

Multicollinearity is not thought to be a problem for several reasons. First, Chow tests in the presence of multicollinearity usually result in the acceptance of the null hypothesis of the equality of regression equations or that differences in the estimated coefficients are statistically insignificant (Maddala 1977). Second, multicollinearity does not pose a problem for estimating capital stock and investment; the estimated equations still permit estimation of the conditional mean.[11]

The equations for the real or deflated value of capital were used to estimate total capital stock and investment for the New England fleet between 1965 and 1981. The real capital stock equations were applied to vessel data available from the Northeast Fisheries Center, and total capital stock was calculated as the sum of the stock over all vessels. Aggregate net investment was calculated as the difference in total capital stock between consecutive years.

Prior to estimating total capital stock and investment, it was necessary to define vessel type by gear to avoid double counting which might occur since vessels frequently switch port and gear. Three categories of gear types were established: 1) otter trawl, 2) scallop dredge, and 3) all others, which include lobster trawl and pots, herring gear, harpoons, etc. Vessels were assigned a gear type based on a plurality of days at sea. Estimates of capital stock and investment are presented in Table 5.

Several limitations should be considered when evaluating the estimates. First, there is the previously discussed problem that estimates of capital stock may be biased or overestimated. Second, estimates are only for New England vessels or those which are believed to be homeported in New England. Third, the capital stock and investment series pertain to New England and not the United States; that is, estimates should not be interpreted as net changes in the capital stock and investment in U.S. fisheries. Fourth, under-

TABLE 5.—Estimates of real capital stock and investment in New England harvesting sector, 1965–81.[1]

| Year | Number of vessels | Capital stock | | | Investment | | | Index of investment |
|---|---|---|---|---|---|---|---|---|
| | | Trawl | Dredge | Other | Trawl | Dredge | Other | |
| | | $ Millions | | | | | | |
| 1965 | 594 | 25.96 | 16.29 | 1.98 | | | | |
| 1966 | 619 | 28.84 | 14.75 | 2.82 | 2.88 | −1.54 | 0.84 | 100 |
| 1967 | 628 | 39.37 | 11.42 | 1.63 | 10.53 | −3.33 | −1.19 | 276 |
| 1968 | 610 | 28.65 | 15.43 | 1.68 | −10.72 | 4.01 | 0.05 | −301 |
| 1969 | 602 | 29.22 | 12.92 | 1.29 | 0.57 | −2.51 | −0.39 | −107 |
| 1970 | 607 | 25.61 | 8.29 | 1.37 | −3.61 | −4.63 | 0.08 | −374 |
| 1971 | 620 | 23.65 | 12.80 | 1.47 | −1.96 | 4.51 | 0.10 | 122 |
| 1972 | 655 | 27.01 | 7.74 | 4.70 | 3.36 | −5.06 | 3.23 | 70 |
| 1973 | 666 | 28.42 | 7.12 | 5.13 | 1.42 | −0.62 | 0.43 | 56 |
| 1974 | 695 | 21.26 | 4.19 | 6.40 | −7.17 | −2.93 | 1.27 | −405 |
| 1975 | 737 | 29.04 | 5.15 | 8.48 | 7.78 | 0.96 | 2.08 | 496 |
| 1976 | 783 | 20.73 | 7.72 | 8.16 | −8.31 | 2.57 | −0.32 | −278 |
| 1977 | 836 | 28.86 | 14.19 | 7.86 | 8.13 | 6.47 | −0.30 | 656 |
| 1978 | 881 | 37.45 | 12.85 | 8.65 | 8.59 | −1.34 | 0.79 | 369 |
| 1979 | 1,107 | 45.41 | 27.30 | 11.25 | 7.96 | 14.45 | 2.60 | 1147 |
| 1980 | 1,260 | 52.26 | 34.30 | 11.69 | 6.85 | 7.00 | 0.44 | 656 |
| 1981 | 1,246 | 43.35 | 30.15 | 11.60 | −8.91 | −4.15 | −.09 | −603 |

[1] Real investment and capital are deflated with producer price index for heavy machinery. 1967 = 100

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[11] For additional information on the problems of multicollinearity with respect to analysis and prediction, see Kmenta (1971).

tonnage vessels or those which are <5 gross registered tons are excluded since data are unavailable; thus, total capital stock and investment in New England fisheries are underestimated.

Despite these limitations, the results provide information on investment and capital stock in New England fisheries which has not been available. As is characteristic of open-access fisheries, investment in New England fisheries appears to have increased over time. This is quite evident subsequent to the passage of the Magnuson Fisheries Conservation and Management Act of 1976. While possibly true, the observation that investment increased when the act was passed should not be construed to imply that the act was responsible for increased investment. Positive expectations regarding fish stocks or economic conditions could also be responsible for increases in capital stock and investment.

The largest increase in investment occurred in 1979 which coincided with the greatest influx of vessels. It also coincided with increased fish stocks in 1978 and 1979 and high vessel profits of the previous year. In 1979, 226 vessels entered the New England fisheries; 92 vessels were newly constructed.

Disinvestment also occurred, but the reasons are unknown.[12] Disinvestment may be associated with vessel sinkings, foreclosures on vessel mortgages, and exit from the region. Alternatively, if vessel prices reflect the expected net discounted present value of earnings from a fishery, the disinvestment or even changes in investment may be due to changes in economic expectations. Disinvestment occurred between 1968 and 1970, 1974, 1976, and in 1981.

Disinvestment between 1968 and 1970 may reflect expectations of declining future earnings. Disinvestment in 1974 may reflect the effects of high fuel prices. Disinvestment in 1976 and 1981 may be associated with fishermen's expectations of declining fish stocks, the effects of management, and high fuel prices.

The reasons for investment are also unknown. Increasing levels of investment between 1977 and 1980 may be due to economic expectations associated with fisheries management, fish stocks, and future earnings.

The real capital stock increased approximately 6% per year between 1965 and 1981. The largest increase occurred in 1978 and 1979 when there was a substantial increase in the number of new steel-hulled vessels and entry of vessels from the mid-Atlantic region. Capital stock declined in 1981 when some of the mid-Atlantic vessels left New England and the stocks of fish, particularly sea scallops, declined (Northeast Fisheries Center 1985).

The results also indicate why a vessel count should not be used to indicate capital stock or investment. The number of vessels increased between 1969 and 1970 and 1975 and 1976, but investment decreased in 1970 and 1976 (Table 6). Alternatively, the number of vessels increased in each year relative to 1965, but the real capital stock between 1969 and 1976 declined with respect to 1965.

TABLE 6.—Indices of capital stock based on constant dollar value and vessel count.

| | Capital stock | | | | | |
|---|---|---|---|---|---|---|
| | Constant dollar value | | | Vessel count | | |
| Year | Trawler[1] | Dredge[1] | Total | Trawler[1] | Dredge[1] | Total |
| 1965 | 100 | 100 | 100 | 100 | 100 | 100 |
| 1966 | 111 | 91 | 105 | 102 | 94 | 104 |
| 1967 | 152 | 70 | 119 | 109 | 77 | 106 |
| 1968 | 110 | 95 | 103 | 104 | 106 | 103 |
| 1969 | 113 | 79 | 98 | 104 | 106 | 101 |
| 1970 | 99 | 51 | 80 | 108 | 74 | 102 |
| 1971 | 91 | 79 | 86 | 108 | 83 | 104 |
| 1972 | 104 | 48 | 89 | 108 | 74 | 110 |
| 1973 | 109 | 44 | 92 | 105 | 79 | 112 |
| 1974 | 82 | 26 | 72 | 107 | 49 | 117 |
| 1975 | 112 | 32 | 96 | 105 | 66 | 124 |
| 1976 | 80 | 47 | 83 | 109 | 202 | 132 |
| 1977 | 111 | 87 | 115 | 107 | 202 | 141 |
| 1978 | 144 | 79 | 133 | 116 | 189 | 148 |
| 1979 | 175 | 168 | 190 | 137 | 313 | 186 |
| 1980 | 201 | 211 | 222 | 158 | 440 | 212 |
| 1981 | 167 | 185 | 192 | 158 | 413 | 210 |

[1] Gear type assigned by plurality of days absent.

The inadequacy of using vessel count is more pronounced when comparing the indices based on gear type. As shown in Table 6, the number of trawl vessels in every year exceeded the number of vessels in 1965 while capital stock was less than that of 1965 for four years. The two scallop dredge indices also indicate dissimilar changes between vessel count and real capital stock. It may, though, be possible than an index based on vessel count and weighted by vessel size would more closely compare to the real capital stock index. The construction of these indices would require considerable additional analysis and determination of the weights necessary for aggregation.

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[12] Hirshleifer (1970) provided additional information about disinvestment.

## SUMMARY AND CONCLUSIONS

This study developed procedures for estimating the capital stock and net investment using only the information generally available. That is, data on acquisition and list prices for some but not all vessels and characteristics for most vessels in a fleet were used to estimate capital stock and investment in a fishery. An hedonic approach which specified the acquisition price as a function of vessel characteristics was suggested as a possible method for obtaining information necessary for estimating capital stock and net investment. It was argued that the approach was consistent with procedures used by economists to estimate the capital stock and investment in traditional industries.

Estimates were based on 1,110 observations obtained from NMFS and classified advertisements for the period 1965–81. Vessel characteristics pertaining to size and age were shown to be the more significant characteristics for explaining the value of a vessel. The corresponding information was then used to estimate the capital stock and investment in the New England fisheries.

An interesting result was that although investment increased over time, there also was disinvestment in the fisheries. It was suggested that this was possibly the result of vessel sinkings, exit of vessels from the region, foreclosures, and expectations of declining future net returns.

It also was demonstrated that a vessel count should not be used to indicate capital stock or investment. The number of vessels generally increased over time, but the level of capital stock did not coincide with these changes. This suggests that more attention should be given to developing economic measures of capital stock and investment.

A question still in need of attention, however, cannot be answered from this study. That is, given the level of investment, can an optimal utilization and allocation of resources be determined. The answer is clearly no. This requires management authorities to specify the objectives of fisheries management and a detailed bioeconomic model.

There is a need for more research on investment, and in particular, the determination of the optimum rate of investment. This includes research on the social discount rate, reasons for investment, and the marginal productivity of capital. More important, additional research is required to better address the issues of fisheries management, particularly whether or not public expenditures should be allocated to managing fisheries.

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## LITERATURE CITED

BAUMOL, W. J.
1977. Economic theory and operations analysis. Prentice-Hall, Englewood Cliffs, N.J.

BLACKORBY, D., D. PRIMONT, AND R. R. RUSSEL.
1978. Duality, separability, and functional structure: theory and economic applications. North-Holland Publishing Company, Amsterdam.

BOCKSTAEL, N. E., W. M. HANNEMANN, AND I. E. STRAND.
1986. Measuring the benefits of water quality improvements using recreation demand models. Volume II of benefit analysis using indirect or imputed market methods. EPA contract No. CR-811043-01-0. U.S. Environmental Protection Agency, Washington, D.C.

BOX, G. E. P., AND D. R. COX.
1962. An analysis of transformations (with discussion). J. R. Stat. Soc., Ser. B:211–243.

BRAEUTIGAM, R. R., A. F. DAUGHETY, AND M. A. TURNQUIST.
1982. The estimation of a hybrid cost function for a railroad firm. Rev. Econ. Stat. 64:394–404.

BRANSON, W. H.
1972. Macroeconomic theory and policy. Harper & Row, Publishers, N.Y.

CHARLES, A. T.
1983a. Optimal fisheries investment:comparative dynamics for a deterministic seasonal fishery. Can. J. Fish. Aquat. Sci. 40:2069–2079.
1983b. Optimal fisheries investment under uncertainty. Can. J. Fish. Aquat. Sci. 40:2080–2091.

CHOW, G. C.
1960. Tests of equality between subsets of coefficients in two linear regressions. Econometrica 28:591–607.

CLARK, C. W., F. H. CLARKE, AND G. R. MUNRO.
1979. The optimal exploitation of renewable resource stocks: problems of irreversible investment. Econometrica 47:25–47.

CUNNINGHAM, S., M. R. DUNN, AND D. WHITMARSH.
1985. Fisheries Economics: an introduction. St. Martin's Press, N.Y.

DADKHAH, K. M.
1984. Confidence interval predictions from a logarithmic model. Rev. Econ. Stat. 66:527–528.

DEWAR, M. E.
1983. Industry in trouble: the Federal government and

New England fisheries. Temple University Press, Philadelphia, PA.

DOERINGER, P. B., P. I. MOSS, AND D. G. TERKLA.
1986. The New England fishing economy. The University of Massachusetts Press, Amherst, MA.

GORDON, H. S.
1954. The economic theory of a common property resource: the fishery. J. Polit. Econ. 62:124–142.

GRIFFIN, W. L., J. P. NICHOLS, R. G. ANDERSON, J. E. BUCKNER, AND C. M. ADAMS.
1978. Costs and returns data: Texas shrimp trawlers, Gulf of Mexico 1974–75. Texas A&M Univ., Dep. Agric. Econ. tech. Rep. TAMU-SG-76-601.

GRILICHES, Z.
1971. Hedonic price indexes for automobiles: an econometric analysis of quality changes. *In* Price indexes and quality changes, p. 103–130. Harvard University Press, Cambridge, MA.

HILBORN, R.
1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. 32:2–13.

HIRSHLEIFER, J.
1970. Investment, interest and capital. Prentice-Hall, Englewood Cliffs, NJ.

KENDRICK, J.
1961. Some theoretical issues in capital measurement. Am. Econ. Rev. 51(2):102–111.

KMENTA, J.
1971. Elements of econometrics. Macmilliam Publishing Co., Inc., N.Y.

KIRKLEY, J. E., M. P. PENNINGTON, AND B. E. BROWN.
1982. A short-term approach for analyzing the effects of harvesting quotas. J. Cons. int. Explor. Mer 40:173–175.

KIRKLEY, J. E.
1986. The relationship between management and the technology in a multi-species fishery. Ph.D. Thesis, Univ. Maryland, Collage Park, MD.

LADD, G. W., AND M. B. MARTIN.
1976. Prices and demands for input characteristics. Am. J. Agric. Econ. 58:21–30.

LAU, L. J.
1978. Applications of profit functions. *In* M. Fuss and D. McFadden (editor), Production economics: a dual approach to theory and applications, p. 133–216. North-Holland Publishing Company, Amsterdam.

MADDALA, G. S.
1977. Econometrics. McGraw-Hill Book Company, N.Y.

NATIONAL ACADEMY OF SCIENCES.
1979. Measurement and interpretation of productivity. National Research Council, Washington, D.C.

NORTHEAST FISHERIES CENTER.
1985. Status of the fishery resources off the northeastern United States for 1985. U.S Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-42, 137 p. Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA.

ROSEN, S.
1974. Hedonic Prices and implicit markets:product differentiation in pure competition. J. Polit. Econ. 82:34–55.

SCOTT, A.
1979. Development of economic theory of fisheries regulation. J. Fish. Res. Board Can. 36:725–741.

SISSENWINE, M. P., AND J. E. KIRKLEY.
1982. Fishery management techniques:practical aspects and limitations. Mar. Policy 6:22–42.

SLOAN, H. S., AND A. J. ZURCHER.
1968. Dictionary of economics. Barnes & Noble, Inc., N.Y.

SMALLWOOD, D. M., AND J. R. BLAYLOCK.
1986. Forecasting performance of models using the Box-Cox transformation. Agric. Econ. Res. 38:14–24.

TETTEY, E. O., W. L. GRIFFIN, J. B. PENSON, AND J. R. STOLL.
1986. Implications of tax policy on investment in a common property resource. N. Am. J. Fish. Manage. 6:100–104.

TRIPLETT, J.
1986. The economic interpretation of hedonic methods. Surv. Curr. Bus. 66:36–40.

VARIAN, H. R.
1984. Microeconomic analysis. 2d, ed. W. W. Norton & Company, N.Y.

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# Effects of Cold Shock on Egg, Larval, and Juvenile Stages of Tropical Fishes: Potential Impacts of Ocean Thermal Energy Conversion

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## *ABSTRACT*

*Ocean thermal energy conversion (OTEC) facilities will bring large volumes of deep, cold water to the surface, where it will be mixed with warm surface water after the utilization of the thermal differential. Mixing of these two water types will result in exposure of larval and juvenile fishes entrained in the warm water intake to lowered temperatures. A time course of cold shock from simulated entrainment was used to determine potential effects upon egg and larval mahimahi,* Coryphaena hippurus, *manini,* Acanthurus triostegus, *and juvenile striped mullet,* Mugil cephalus. *Experiments were designed to test varying exposure times and temperature changes upon different early life stages of tropical fishes.*

*Earlier stage eggs were more sensitive to temperature shock, with mortality increasing with increasing delta T as compared to controls; exposure time, however, did not exert a significant effect. Significant excess mortality for all stages of eggs occurred at the range of times and temperatures used in the experiments, although in some cases these exceed values proposed in current OTEC engineering plans. For mahimahi larvae, excess mortality increased with age to values higher than for latest stage eggs, but we consider this to be caused by stress associated with yolk exhaustion. A single size range of juvenile mullet was exposed to the same experimental protocol as the eggs and larvae. Although exposure time was not significant, delta T had a significant effect upon mortality, and there was a significant interaction between exposure time and delta T.*

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## INTRODUCTION

Studies on man-induced thermal effects on aquatic ecosystems have generally considered elevated temperatures resulting from once-through cooling systems of fossil fuel or nuclear power-plants (Van Winkle, 1977; Schubel *et al.*, 1978; Talmage & Coutant, 1979). The majority of these studies have concentrated on higher latitude marine and freshwater ecosystems (Hoss *et al.*, 1974; Burton *et al.*, 1976; Smith *et al.*, 1979; Barker *et al.*, 1981). As the utilization of marine waters for cooling increased, concerns about negative impacts upon fisheries developed (Saila, 1975). Most studies of thermal effects in marine systems have concentrated upon elevated temperatures; the proposed development of ocean thermal energy conversion (OTEC), however, raises new concerns about exposure to decreased temperatures in the effluent plume (Myers *et al.*, 1986). Hoss *et al.* (1986) studied the effects of decreased temperature on juvenile French grunt and observed no major mortality effects at temperatures expected from OTEC operations. In this study, we consider the effects of lowered temperatures upon early life history stages of tropical fishes with special attention to egg and larval stages.

Effects of thermal stress on egg and larval stages of fishes are important because ichthyoplankton is vulnerable to entrainment and highly sensitive to temperature fluctuations (Horst, 1975; Schubel, 1975; Rosenthal & Alderdice, 1976). Again, most of these studies have concentrated upon the effects of elevated temperature, primarily as it affects mortality (Smith *et al.*, 1979; Barker *et al.*, 1981). Relatively little work has been conducted upon the lower thermal tolerances of fish larvae or upon the effects of lower temperatures upon development, particularly in tropical systems. Tropical species, however, have less tolerance to cold than do temperate species (Shimada *et al.*, 1985). Even slightly lowered temperatures may have subtle but important effects upon the larval development. Lasker (1964), for example, noted normal development of larval Pacific sardine, *Sardinops caerulea*, at temperatures of 14°–21°C, but no development of a functional jaw at temperatures of 13°C and below. Larvae were unable to initiate feeding at temperatures which were only slightly lower than those observed in nature. Pacific cod (*Gadus macrocephalus*) eggs can tolerate variability in salinity and dissolved oxygen if within a temperature range of 3°–5°C, but egg viability decreased sharply, irrespective of other environmental conditions, below 3°C (Alderdice & Forrester, 1971). Lowered temperatures may also affect the order of appearance of developmental features in embryos (Hayes *et al.*, 1953) and may result in abnormal hatching. Eggs of *Bairdiella icistia* reared at 18°C failed to develop past the blastula stage despite normal embryonic development between 20° and 30°C (May, 1974).

These and other studies demonstrate that temperatures only a few degrees below ambient may cause significant mortality in fish embryos and larvae.

Temperature shocks in nature may also be characterized by sublethal or stress effects, where the probability of subsequent mortality is increased (Rosenthal & Alderdice, 1976; Mazeaud *et al.*, 1977). Sublethal stresses may decrease predator avoidance capabilities in nature (Coutant, 1973; Farr 1977). Coutant *et al.* (1974) observed increased predation in juvenile channel catfish, *Ictalurus punctatus*, and largemouth bass, *Micropterus salmoides*, exposed to varying cold thermal shocks. The incidence of predation increased with increasing magnitude of shock temperatures.

In the present study we describe the effects of lowered temperatures on egg and larval stages of two representative species of tropical marine fishes, the mahimahi, *Coryphaena hippurus*, and the manini, *Acanthurus triostegus*, and on juvenile striped mullet, *Mugil cephalus*. By considering pelagic, reef-dwelling, and nearshore species, the results of these experiments are pertinent to understanding potential thermal effects of OTEC on early life history stages of fishes.

## MATERIALS AND METHODS

Experiments were conducted at the Kewalo Research Facility of the Southwest Fisheries Center Honolulu Laboratory, where the capability to naturally spawn pelagic and reef fishes provided experimental animals. Our experimental design considered an analysis of the time–temperature histories for seawater pumped through and discharged from typical OTEC operations (E. Myers, Ocean Minerals and Energy, NOAA, Washington, DC 20235, pers. comm.). This design (Fig. 1) is patterned after the engineering plans for the Ocean Thermal Corporation's (1983) planned Kahe Point facility. Warm surface water (74·54 m$^3$/s at 25·5°C) is drawn into the plant and immediately mixed with the warm water effluent from the existing oil-fired plant (31·85 m$^3$/s at 31·3°C), raising the temperature of the mixed water to 27·2°C. Flow through the heat exchangers results in a small temperature drop, and mixing of cold and warm water causes the final temperature to drop to approximately 16·7°C. The time for a change from ambient to mixed temperatures is $<1$ min. The transit through the mixed effluent pipes would be approximately 8 min (Fig. 1) before release near a depth of 100 m, where a dilution period of about 1 min would bring the temperature back to within 2°C of the surface temperature.

Attempts were made to simulate representative thermal histories in the experiments, but we did not include the small temperature increase (Fig. 1) associated with the heated effluent addition before thermal shock. In our

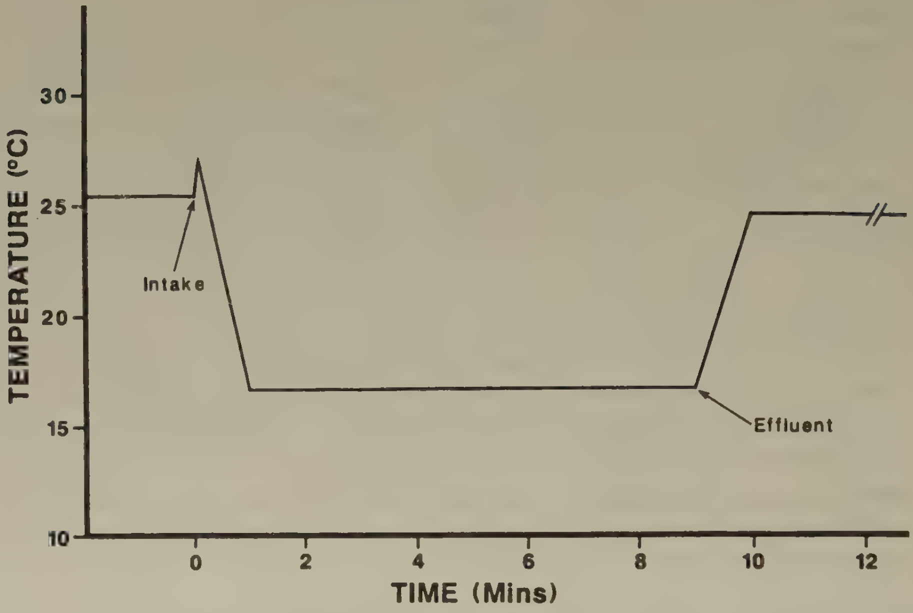

Fig. 1. Time–temperature history for a water parcel or organism entrained into the warmwater intake of the proposed Kahe Point facility (OTC, 1983). At time zero, the water enters the plant, mixes with the heated effluent from the nearby oil-fired plant, decreases in temperature as it proceeds through the heat exchangers and then mixes with the cold water. The mixed effluent takes approximately 8 min to reach the terminus of the pipe, where it gradually increases to the ambient temperature at the release depth (near 100 m).

design, the experimental variables considered are stage of egg or larval development, magnitude of thermal shock (delta T), and duration of lowered temperature exposure. Developmental stage classification for mahimahi was obtained from Palko *et al.* (1982); manini eggs were staged using Oppenheimer's (1937) classifications. We used delta T's of 5°, 10°, and 15°C and exposure times of 8, 16, and 24 min in our experiments. The values for delta T and exposure times exceeded those in Fig. 1, but were chosen to encompass a range that would include alternate plant designs.

Mahimahi brood stock was maintained in various flow-through circular tanks (5 or 7·2 m diameter) at ambient temperatures of 23·5° to 24·5°C. During the course of the experiments, the brood stock spawned every other day without artificial induction. Mahimahi eggs are spherical (1·52–1·66 mm in diameter), buoyant, and have a single oil globule (0·31–0·34 mm in diameter). At an ambient water temperature of 26°C, the eggs hatched approximately 54 h after spawning and larvae ranged from 4·3 to 5·4 mm standard length (SL).

A complete series of experiments for mahimahi was composed of three tests; each test consisted of a single delta T with samples from six developmental stages at three exposure times including a control and replicates. The developmental stages were 0, 12 and 24 h post-fertilization eggs; larvae were at day of hatch, and day 2, and day 4 post hatch. Three exposure times (8, 16 and 24 min) and a control were used for each of three temperature shocks (delta T, 5, 10 and 15 C°) below the ambient temperature (26°C). Three replicate samples for the three exposure times and control resulted in 12 samples per developmental stage per temperature drop (a total of 72 samples per test). Fifty eggs or 20 larvae were tested per replicate. For each test, eggs and larvae used were obtained from a single spawning day. Specific controls for each spawning were necessary because egg quality may vary among spawnings (T. K. Kazama, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396, pers. comm.).

Mahimahi eggs were collected within 10–20 min after spawning. The eggs were gathered in a fine-mesh dip net as they floated along the surface of the water; they were placed in a 22·8-liter (6 gallons) bucket with seawater from the parental tank. The procedure was repeated until 4000–5000 eggs were collected. The eggs were taken into the laboratory and mildly aerated. Samples were removed and checked for normal fertilization and development. They were then placed in a 100-liter rearing tank within a water bath maintained at 26°C. The 100-liter tank and the water bath contained aerated seawater filtered through a 0·22-μm Millipore filter system. A photoperiod with 18 h of light and 6 h of darkness (18L: 6D) was maintained with timers on a fluorescent light system directly above the water bath tank. Marine microalgae (*Tetraselmas* sp. and *Isochrysis* sp.) were added in small quantities to the 100-liter tank and the ambient water bath tank to maintain water quality. On day 1 post hatch, the 100-liter tank was inoculated with rotifers (*Brachionus* sp.) at a concentration of 1–2/ml. This food density was maintained until the termination of the experiments at day 5 post hatch. At 26°C yolk was absorbed by day 2 post hatch.

Eggs and larvae were placed in 1-liter plastic beakers modified for water transfer by cutting six windows symmetrically around the top of the beaker. The windows were covered with 0·35-mm Nitex mesh attached with silicone caulk. Beakers were labeled and the eggs or larvae randomly distributed among the beakers. The beakers were suspended in the ambient temperature (26°C) water bath by rings of styrofoam. A fine-pore airstone was suspended in each beaker and the seawater gently aerated. The beakers to be subjected to the thermal shock were individually transferred from the ambient-temperature, water-bath tank (holding tank) to the treatment tank (shock tank). The shock tank was maintained at the desired temperature for the test—delta T of 5 (21°C), 10 (16°C), or 15 C° (11°C, all ±0·5°C)—by use of a cooling unit in the shock tank.

The transfer was made by allowing the ambient seawater in the beaker to drain to the bottom of the screened window, approximately one-fourth the height of the beaker. It was then placed in the shock tank and the colder seawater allowed to bring the water volume to 1 liter. Then, 4 liters of seawater from the shock tank were siphoned into each 1-liter test beaker through a 5-mm inside diameter (ID) hose. This produced a 1-min temperature drop from the ambient temperature (26°C) to the desired shock temperature. This procedure was repeated for each of nine test beakers per stage exposed to the thermal shock. Controls were handled identically but were placed back into the holding tank.

After the appropriate exposure time in the shock tank, each test beaker was again allowed to drain to the bottom of the screened window, returned to the holding tank, and, over a period of 1 min, flooded with ambient seawater from the water bath to bring the temperature up to 24°C. The beaker was left in the holding tank so that the water temperature could slowly return to the ambient (26°C); this required approximately 1 h. The test beakers were kept in the holding tank at ambient temperature until the termination of the test. The control beakers were handled in the same manner but with no thermal shock.

Eggs were held in the test beakers until day 1 post hatch. Mortality and development data were recorded daily. Approximately 12 h after the thermal shock occurred, eggs exposed to the shock and the control samples were checked for mortalities and incidences of abnormalities as described by Rosenthal & Alderdice (1976). Thereafter, eggs were checked every 24 h until day 1 post hatch for mortality or abnormality. On day 1 post hatch, experiments were terminated; surviving and dead eggs were counted and recorded. Observations of abnormalities in surviving eggs and larvae, as well as time delays in hatching, were also recorded. Methodology for handling larvae was similar. Dead larvae were removed 1 h after the thermal shock, and survivors kept in the test beakers for periods ranging between 16 and 24 h post shock. When the experiment was terminated, the numbers of dead and surviving larvae were recorded.

Manini brood stocks were kept in a 7·2-m diameter tank at ambient temperatures (23·1° to 23·4°C). Various species of tuna were usually also in the tank but did not interfere with the spawning activity of the manini. The brood stock spawned naturally two to three times a week until mid-October, 1984, after which spawning became less frequent (once a week at most). A few days before periods of a full moon, however, spawning activity increased. Manini eggs are spherical, 0·63–0·70 mm in diameter, buoyant, and have a single oil globule (0·15–0·18 mm in diameter). At an ambient seawater temperature of 26°C, the eggs hatched approximately 36 h after spawning and larvae ranged from 2·03 to 2·43 mm SL.

The experimental design was identical to the mahimahi procedures with minor exceptions. Three developmental stages were used for each test (two egg stages, 0 and 18 h post-fertilization, and one yolk sac larval stage, day 1 post hatch); thus, the complete series of experiments consisted of three tests, each with one delta T, three developmental stages at three exposure times with a control, and three replicates of each. Manini eggs were collected within 10–30 min after spawning. The eggs were handled and processed in the same manner as the mahimahi eggs. The experimental beakers were modified by painting the bottoms black to facilitate observations of the small, semitransparent larvae; the windows were covered with 0·25 mm Nitex mesh. The water bath, rather than individual beakers, was aerated. The only microalga used as water conditioner in these experiments was *Isochrysis* sp.

The procedure for treating the smaller eggs and larvae after the thermal shocks differed from mahimahi experiments. The eggs were held in test beakers until day of hatch; mortality data were recorded only at the termination of each experiment. Mortality and survival of eggs and larvae, as well as time delays in hatching, were also recorded at this time. Larvae were held for 24 h post shock; the numbers of survivors were recorded at the termination of experiments. At the termination of each test, all surviving eggs and larvae were labeled and preserved in 3% formalin (in seawater).

Juvenile striped mullet, *Mugil cephalus*, were collected between 8 November and 18 December at Waialae Beach Park, Honolulu, Hawaii, and kept in 2-m circular flow-through tanks in water between 25° and 26°C. They were fed a varied diet including trout and catfish chow, live brine shrimp, *Artemia* sp., and commercial flake fish food. The fish used in the experiments ranged from 25·8 to 66·5 mm SL.

The basic experimental design was similar to that used with larval stages, except that the juvenile experiments were conducted on a larger scale. A complete series of experiments consisted of three tests. Only one stage (juvenile fish) was used in each test, but exposure times and delta T were the same as in larval experiments. Two complete series of experiments were run. In the first series, three replicates were used for each exposure time and control; in the second series, only two replicates were used due to the numbers of fish available. Ten juveniles were used for each replicate.

Juveniles were randomly transferred from outside holding tanks, in groups of five fish, to 38-liter (10 gal) glass aquaria until each tank contained ten fish. A 200-W submersible heater in each tank maintained a 26°C seawater temperature; water was circulated by use of an airstone suspended in each tank. The alga, *Tetraselmas* sp., was added in small quantities to maintain water quality. The fish were allowed to acclimate in the tanks for 4 to 5 h before the exposure experiments were conducted. Fish in tanks to be subjected to the thermal shock were transferred to a 4-liter bucket 5 min before the exposure. The buckets were modified to facilitate water exchange; each bucket had 3-mm holes uniformly cut from the top to the 1·5-liter level. Transfer to the shock tank involved gradual immersion of the bucket into the colder seawater to produce a 1-min temperature drop from the ambient temperature.

Two minutes before termination of the exposure, cold seawater was added to the holding tanks to reduce the temperature to 24°C. After the appropriate exposure time for each sample, buckets were drained to the 1·5-liter mark and gradually submerged and flooded with seawater in the holding tank to bring the test fish to 24°C in 1 min. The heaters raised the temperature to 26°C over a period of 30 min to 1 h. The control fish were handled in the same way, except that the water was maintained at the ambient temperature (26°C). The fish were kept in the holding tanks for 24 to 48 h post shock.

Data analysis consisted of three-way analysis of variance (ANOVA) with Duncan's multiple range test (Nie *et al.*, 1975) to compare treatment means. Two ANOVA's were run for each experiment. The data analyzed in the first were proportion survival, with factors delta T (three levels), stage of development (varying levels by taxa), and exposure time (four levels, where controls represented zero exposure time). In the second ANOVA, the datum analyzed was proportion excess mortality. Control mortality varied with egg quality; past experience with mahimahi shows that egg viability varies from day to day. To adjust for this variability, mean mortality values for controls were subtracted from the relevant treatment values to determine 'excess mortality'. Both values, as proportions, were arcsin transformed before running the ANOVA.

## RESULTS

### *Coryphaena hippurus*, Mahimahi

Five complete tests were conducted using six stages of mahimahi eggs and larvae with three tests at 5 C°, one test at 10 C°, and one test at 15 C°. For 0 h post-fertilization eggs, delta T of 10 and 15 C° produced 100% mortalities irrespective of exposure times (Fig. 2a), generally within 12 h of exposure to the cold shock. These eggs, shocked between the 2 and 16 cell stage, failed to develop beyond the gastrula stage and died. The control eggs, from the same age group, however, were developing normally and at the early neurula stage. Newly fertilized eggs exposed to 5 C° delta T had higher excess mortalities than later stages exposed to the same delta T and exposure time. The 12 h post-fertilization eggs were shocked at the late gastrula–early neurula stage. Again, the greatest excess mortalities were observed at delta

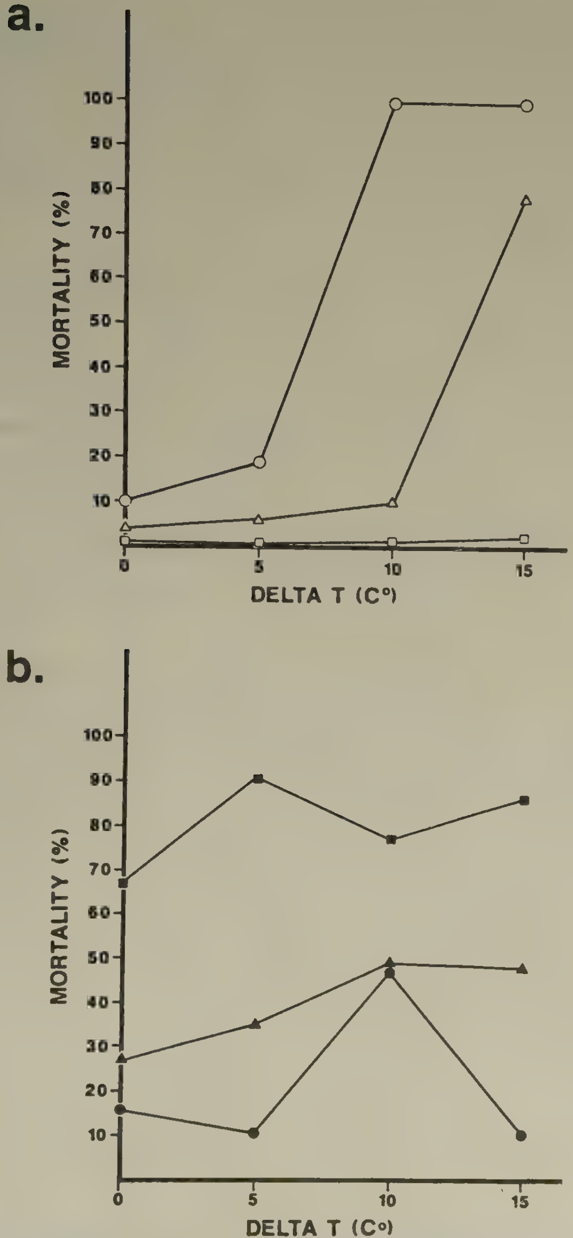

**Fig. 2.** Results of thermal exposure experiments on egg (a) and larval (b) stages of mahimahi, *Coryphaena hippurus*. Each data point is the mean of three replicates at each exposure time with the exception of the delta T 5 C° and the controls (delta T 0 C°); the former is based upon three experiments and the latter upon the mean of controls run each day. Actual data points were arcsin transformed before taking means and means were transformed back to percentage mean mortalities. ○ = 0 h post-fertilization; △ = 12 h post-fertilization; □ = 24 h post-fertilization. ● = day-of-hatch; ▲ = day 2; ■ = day 4.

T 15 C°, and mortality decreased at the lower delta T's (Fig. 2(a)). The 24-h post-fertilization eggs were exposed to thermal shock at the developing embryo stage; the embryo occupied approximately one-half the circumference of the egg, the optic vesicles were formed, and the yolk was pigmented. Excess mortality of the eggs exposed at this stage was significantly lower than eggs exposed at earlier stages and not significantly different from controls. Excess mortality increased slightly, however, in eggs exposed to greater delta T's.

In all the egg stages shocked and reared to hatching in the 1-liter beakers, some deaths were observed on the day of hatch. Abnormalities were also observed in these experiments and included yolk and oil globule deformities, bent body, tail and head deformities, and an amorphous embryo mass. Abnormalities in 0-h post-fertilization eggs were more common than in eggs exposed to cold thermal shock at later stages; the incidence of abnormalities in the 12-h post-fertilization eggs was greater than that in eggs shocked at 24 h post-fertilization. The 12- and 24-h stage egg data could not effectively be compared to the 0-h stage egg data due to the 100% mortalities at the higher delta T's (Fig. 2(a)). The percentage of abnormalities in the 24-h post-fertilization tests, however, was very low.

The results for the larval stages were almost inverse to that seen for the egg stages. The newly hatched larvae generally had lower excess mortalities than day 2 and day 4 post-hatch feeding larvae but neither the delta T nor exposure time significantly affects the survival of the day-of-hatch larvae (Fig. 2(b)). The day 2 and day 4 larvae have significantly higher mortality than day-of-hatch larvae, but excess mortality is not significantly different due to high mortalities in the controls (Table 1). In our experiments, all larvae showed similar reactions to the cold shock; they turned slightly dark, sank to the bottom of the beaker, and were less active. When returned to the ambient temperature water bath, they quickly resumed their normal coloration and position in the water column. The degree and speed of their response to the cold thermal shock were directly proportional to the magnitude of delta T. The greater mortalities seen in day 2 and day 4 larvae may have been a result of starvation. Although the larvae were fed before the experiments, lack of food could have resulted in sublethal stress within the 24-h post shock period; the excess mortalities (Table 1) may have been the result of the additional stress of the thermal shock.

Analyses of the mahimahi egg and larva data, including the treatment of eggs and larvae separately and combined, are presented in Table 1. Interaction effects of the factors were not considered. Generally, the ANOVA analysis on the excess mortality most clearly demonstrates the important effects. Overall, the most significant effects were from delta T and developmental stage; exposure time had no effect (the effect of exposure

TABLE 1

Thermal Exposure Experiment on Mahimahi, *Coryphaena hippurus*, Egg and Larval Stages. Three-way ANOVA and Duncan Multiple Range Test Summary. Results Shown are from Arcsin Transformation Data Analysis which have been Converted Back to Per Cent Mean Mortality and Per Cent Excess Mortality. The Results of the Three-way ANOVA and Duncan Multiple Range Test are given for the Three Experimental Variables: Delta T, Developmental Stage, and Exposure. Duncan Multiple Range Test: $x$ = Mean; D–G = Duncan Grouping, Means with the Same Letter are not Significantly Different. Three-way ANOVA Analysis: PR > $F$ Values, $\geq 0{\cdot}05$ = NS; $< 0{\cdot}05$ = *; $\leq 0{\cdot}01$ = **; $\leq 0{\cdot}001$ = ***.

| *Variable* | | *Mahimahi combined* | | | | | | *Mahimahi eggs* | | | | | | *Mahimahi larvae* | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Mean mortality* (%) | | | *Excess mortality* (%) | | | *Mean mortality* (%) | | | *Excess mortality* (%) | | | *Mean mortality* (%) | | | *Excess mortality* (%) | | |
| | | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* |
| Delta T (C°) | 5 | 17·82 | C | | 13·64 | B | | 5·42 | C | | 7·13 | C | | 36·06 | B | | 19·94 | A | |
| | 10 | 32·07 | B | *** | 34·42 | A | *** | 15·22 | B | *** | 46·63 | B | *** | 53·66 | A | * | 21·60 | A | NS |
| | 15 | 37·58 | A | | 37·27 | A | | 34·76 | A | | 57·64 | A | | 40·48 | B | | 14·89 | A | |
| Developmental stage | | | | | | | | | | | | | | | | | | | |
| Egg | 0 h | 34·63 | B | | 52·47 | A | | 34·63 | A | | 52·47 | A | | — | — | — | — | — | — |
| | 12 h | 12·32 | C | | 20·29 | B | | 12·32 | B | *** | 20·29 | B | *** | — | — | — | — | — | — |
| | 24 h | 0·24 | D | *** | 0·83 | C | | 0·24 | C | | 0·83 | C | | — | — | — | — | — | — |
| Larvae | DOH | 12·86 | C | | 16·63 | B | | — | — | — | — | — | — | 12·86 | C | | 16·63 | A | |
| | Day 2 | 36·68 | B | | 17·55 | B | *** | — | — | — | — | — | — | 36·68 | B | *** | 17·55 | A | NS |
| | Day 4 | 81·44 | A | | 23·73 | B | | — | — | — | — | — | — | 81·44 | A | | 23·73 | A | |
| Exposure | 8 min | 25·86 | A | | 20·29 | A | | 13·01 | A | | 23·07 | B | | 42·30 | A | | 17·49 | A | |
| | 16 min | 26·48 | A | *** | 22·58 | A | NS | 14·36 | A | *** | 26·71 | A | NS | 40·92 | A | ** | 18·59 | A | NS |
| | 24 min | 31·80 | A | | 23·65 | A | | 15·33 | A | | 25·45 | A, B | | 50·42 | A | | 21·85 | A | |
| | Control | 13·31 | B | | — | — | | 3·91 | B | | — | — | | 27·72 | B | | — | — | |

time in the analysis of percentage mean mortality is significant, but this is due to the inclusion of controls as zero exposure time; this group is significantly less in all cases but treatment means are equal). The effects of delta T were apparent for all data combined and for eggs, but not for larvae alone. For the combined analysis, the 5 C° differed from the 10 and 15 C° data, whereas for the eggs, the treatment means increased with increasing delta T. As a function of developmental stage, in the combined analysis, excess mortality for newly fertilized eggs is significantly greater than that for the group with 12-h eggs and all three larval groups; the 24-h post-fertilization eggs suffer significantly lower excess mortality than either group. For eggs alone, each group differs in the same manner as in the combined analysis, whereas the larval groups analyzed alone are not significantly different.

### *Acanthurus triostegus*, Manini

Three complete tests, one at each delta T, were conducted using the three stages of manini eggs and larvae. The results (Fig. 3) were similar to those in

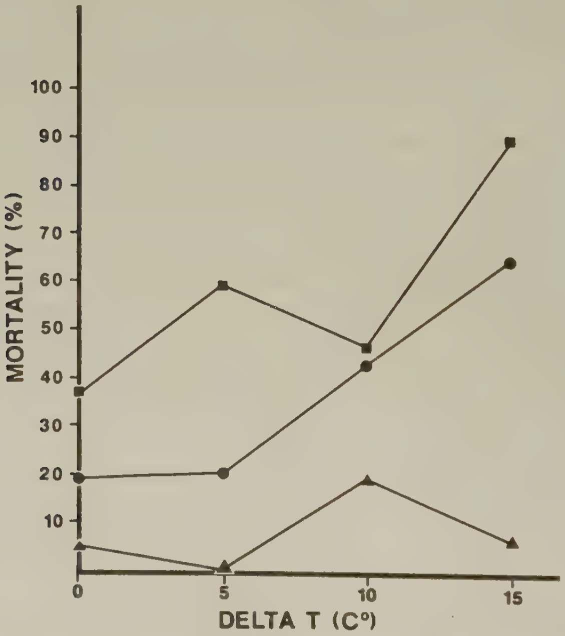

Fig. 3. Results of thermal exposure experiments on egg and larval stages of manini, *Acanthurus triostegus*; data points are means across exposure times. Actual data points were arcsin transformed before taking means and means were transformed back to percentage mean mortalities. Egg stages: ● = 0 h post-fertilization; ▲ = 18 h post-fertilization. Larval stage: ■ = day 1.

the mahimahi experiments. For newly hatched eggs, mortalities increased with increasing delta T. The later egg stage (18-h post-fertilization) had greatly decreased mortalities at all delta T's. The day 1 yolk sac larvae, including the controls, showed very high mortalities (Fig. 3); when calculated as excess mortality, no trends related to delta T's or exposure period were apparent. The manini data showed significant effects of all variables when mean per cent mortality data were included, but exposure time was not significant when considering excess mortality (Table 2). Percentage excess mortality for 5 and 10 C° delta T was not significantly different, but both differed from 15 C° delta T. The only significant effect of development stage was that 18-h post-fertilization eggs had a very low mortality compared to early stage eggs or yolk sac larvae (Table 2).

## *Mugil cephalus*, Mullet

The juvenile mullet were used in two complete series of experiments. In the first series, larger fish (mean 50·1 mm SL) were used in three tests at each

TABLE 2

Thermal Exposure Experiment on Manini, *Acanthurus triostegus*, Egg and Larval Stages. Three-way ANOVA and Duncan Multiple Range Test Summary. Results shown are from Arcsin Transformation Data Analysis which have been Converted Back to Per Cent Mean Mortality and Per Cent Excess Mortality. The Results of the Three-way ANOVA and Duncan Multiple Range Test are given for the Three Experimental Variables: Delta T, Developmental Stage, and Exposure. Duncan Multiple Range Test: $x$ = Mean; D–G = Duncan Grouping, Means with the Same Letters are Not Significantly Different. Three-way ANOVA Analysis: PR > $F$ Values, ≥0·05 = NS; <0·05 = *; ≤0·01 = **; ≤0·001 = ***

| *Variable* | | *Mean mortality* (%) | | | *Excess mortality* (%) | | |
|---|---|---|---|---|---|---|---|
| | | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* |
| Delta T (C°) | 5 | 17·21 | B | | 9·69 | B | |
| | 10 | 32·81 | A | *** | 11·88 | B | *** |
| | 15 | 33·40 | A | | 37·39 | A | |
| Developmental stage | | | | | | | |
| Egg | 0 h | 34·48 | B | | 28·98 | A | |
| | 18 h | 4·27 | C | *** | 3·78 | B | *** |
| Larvae | Day 1 | 56·58 | A | | 26·43 | A | |
| Exposure | 8 min | 31·26 | A | | 20·69 | A | |
| | 16 min | 31·21 | A | *** | 20·67 | A | NS |
| | 24 min | 31·78 | A | | 18·17 | A | |
| | Control | 16·55 | B | | — | — | |

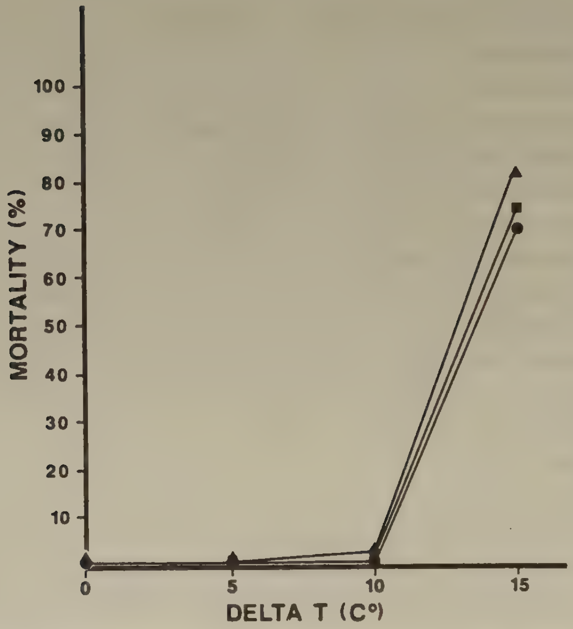

**Fig. 4.** Results of thermal exposure experiments on juvenile striped mullet, *Mugil cephalus*; data points are means across exposure times. Actual data points were arcsin transformed before taking means and means were transformed back to percentage mean mortalities. Each data point is the mean of five replicates. ● = Experiment I; ▲ = Experiment II; ■ = Experiment I and II combined.

delta T with three replicates. In the second series, smaller fish (mean 33·0 mm SL) were used with two replicates. The size difference between the groups of fish was significant (*t*-test, $P < 0{\cdot}01$), but there was no significant difference in excess mortality (*t*-test, $P > 0{\cdot}05$); data from both series of experiments were thus combined. The juvenile mullet showed no significant excess mortality at 5 and 10 C° delta T (Fig. 4). Behaviorally, juveniles placed into the cold shock at those temperatures typically turned dark, decreased activity, and remained near the bottom of the container. A few of the fish at 10 C° delta T swam in quick, jerking motions for a few seconds before settling like the others. At 15 C° delta T, however, the fish placed in the water swam in similar quick jerking motions with their opercula flared and lost equilibrium after a few seconds. Most of the fish that exhibited this behavior did not recover and died; 25% of the fish did recover and survived to the end of the experiment (Table 3). In general, the behavior patterns of fish exposed to this thermal shock was much like that described in Hoss *et al.* (1986). In these experiments, unlike the ones above, exposure time did have a significant effect on excess mortality within the 15 C° delta T. As the exposure time increased, excess mortality also increased (Table 3).

TABLE 3

Thermal Exposure Experiment on the Striped Mullet, *Mugil cephalus*, Juvenile Stage. Three-way ANOVA and Duncan Multiple Range Test Summary. Results shown are from Arcsin Transformation Data Analysis which have been Converted back to Per Cent Mean Mortality and Per Cent Excess Mortality. The Results of the Three-way ANOVA and Duncan Multiple Range Test are Given for the Three Experimental Variables: Delta T, Developmental Stage, and Exposure. Duncan Multiple Range Test: $x$ = Mean; D–G = Duncan Grouping, Means with the Same Letter are Not Significantly Different. Three-way ANOVA Analysis: PR > $F$ Values, ≥0·05 = NS; <0·05 = *; ≤0·01 = **; ≤0·001 = ***

| *Variable* | | *Mean mortality* (%) | | | *Excess mortality* (%) | | |
|---|---|---|---|---|---|---|---|
| | | *x* | *D–G* | *ANOVA* | *x* | *D–G* | *ANOVA* |
| Delta T (C°) | 5 | 0·10 | B | | 0·33 | B | |
| | 10 | 0·15 | B | *** | 2·01 | B | *** |
| | 15 | 43·92 | A | | 79·81 | A | |
| Exposure | 8 min | 9·61 | A | | 21·65 | A | |
| | 16 min | 10·47 | A | *** | 35·97 | A | NS |
| | 24 min | 12·23 | A | | 35·36 | A | |
| | Control | 0·05 | B | | — | — | |

## DISCUSSION

Survival of fishes through early life history stages is an important aspect of population dynamics; oviparous fishes which produce large numbers of small eggs obviously suffer high mortality in early life history stages, primarily from starvation and predation (Hunter, 1976, 1981). Environmental perturbation or pollution may clearly increase mortalities during these early life history stages through either direct effects (Hunter *et al.*, 1979; Longwell & Hughes, 1981) or sublethal effects (Rosenthal & Alderdice 1976). Thermal pollution, depending upon the magnitude, may be either lethal or sublethal to aquatic organisms.

High temperatures, such as those encountered in typical nuclear or oil-fired electrical generation operations, have been shown to have potentially negative impacts upon early life history stages of marine fishes (Smith *et al.*, 1979; Talmage & Coutant, 1979; Barker *et al.*, 1981). These studies, however, have typically been conducted in temperate regions, where fishes may be more eurythermal than in tropical regions. Concern over cold shock in these regions has mainly related to mortality of animals in warm effluent plumes during periods of electrical plant shutdown in winter (Ash *et al.*, 1974; Pilati, 1976); these impacts are typically of short duration and occur locally. Fish kills from either cold weather or intrusions of cold water have been documented in tropical regions (Bohnsack, 1983), demonstrating that tropical fishes generally have less tolerance to low temperature shock than temperate fishes. Furthermore, acclimation to low temperature is typically slower than to high temperature (Doudoroff, 1942). Early life history stages of fishes may also be adapted to the upper range of temperatures experienced by a species, as shown by laboratory (Medvick & Miller, 1979), distributional (Norris, 1963), and growth and energetics studies (Boehlert, 1982; Boehlert & Yoklavich, 1983). Thus, cold shock may exert a strong negative effect upon early life stages of tropical fishes (Shimada *et al.*, 1985).

Our results suggest that lowered temperatures likely to be encountered by a fish egg or larva in currently proposed OTEC operations (Fig. 1) may cause slightly increased mortalities. The highest excess mortalities due strictly to the thermal effects occur for the earliest developmental stages of eggs for mahimahi (Fig. 2(a) and (b); Table 1) and manini (Fig. 3; Table 2), whereas later stage eggs suffer less thermal mortality. The highest mortalities occur at delta T greater than that currently proposed for OTEC operations (Fig. 1); alternate designs, however, could conceivably produce greater temperature drops. Low hatching rates for Atlantic menhaden eggs and low survival of early larvae occur at 12°C, whereas 15 mm larvae can withstand 3·5°C (W. F. Hettler, Jr, NMFS Beaufort Laboratory, Beaufort, NC, pers. comm., 29 May 1987). Thus, eggs and newly hatched larvae may be relatively stenothermal and become more eurythermal during development. Larvae show particularly high mortality in later stages, but this occurs in the controls as well, implicating either problems with the rearing system or starvation-related effects. Nonetheless, the significant excess mortalities in the larval stages suggest that sublethal effects may be exerted upon these stages, making the probability of subsequent mortality higher (Mazeaud *et al.*, 1977). For the juvenile mullet considered in this study, significant mortality was only observed at delta T 15 C° (Fig. 4). This is considerably higher than planned temperature changes for a parcel of water entrained in the warmwater intake (Fig. 1) and thus older stages may be tolerant of the lowered temperatures likely to be encountered. Furthermore, juvenile stages will be better able to avoid either entrainment or low temperature conditions in the environment. These results agree with conclusions of Hoss *et al.* (1986).

Entrainment of fish eggs or larvae through an OTEC facility would result in several stresses, including thermal (Fig. 1), pressure and mechanical effects, exposure to biocides, and displacement from preferred habitat. Matsumoto (1984) suggested that these effects would result in 100% mortality of entrained fish eggs and larvae. Our results suggest that the thermal stresses alone will not result in such high mortality, but synergism of thermal effects with the other direct impacts (Hoss *et al.*, 1977) may result in high mortalities before the larvae leave the system in the effluent. Koo & Johnson (1978) suggested that mortality and hatchability are not sufficiently good criteria of thermal shock in eggs, since thermal shock increased larval deformities. Such sublethal effects, including developmental anomalies, deformation, increased vulnerability to predation, and displacement from feeding areas are all possible impacts from lowered temperature not considered relative to OTEC operations.

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## REFERENCES

Alderdice, D. F. & Forrester, C. R. (1971). The effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). *J. Fish. Res. Board Can.*, **28**, 883–901.

Ash, G. R., Chymko, N. R. & Gallup, D. N. (1974). Fish kill due to 'cold shock' in Lake Wabamun, Alberta. *J. Fish. Res. Board Can.*, **31**, 1822–4.

Barker, S. L., Townsend, D. W. & Hacunda, J. S. (1981). Mortalities of Atlantic herring, *Clupea h. harengus*, smooth flounder, *Liopsetta putnami* and rainbow smelt, *Osmerus mordax*, larvae exposed to acute thermal shock. *Fish. Bull., U.S.*, **79**, 198–200.

Boehlert, G. W. (1982). Ontogenetic changes in growth and their relationship with temperature and habitat change. In *GUTSHOP '81: Fish Food Habits Studies.* ed. G. M. Cailliet & C. A. Simenstad, *Proceedings of the Third Pacific Workshop, December 6–9, 1981, Pacific Grove, California.* Washington Sea Grant Program, University of Washington, Seattle, WSW-WO 82-2, pp. 115–23.

Boehlert, G. W. & Yoklavich, M. M. (1983). Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. *Environ. Biol. Fishes*, **8**, 17–28.

Bohnsack, J. A. (1983). Resiliency of reef fish communities in the Florida Keys following a January, 1977 hypothermal fish kill. *Environ. Biol. Fishes*, **9**, 41–53.

Burton, D. T., Richardson, L. B., Margrey, S. L. & Abell, P. R. (1976). Effects of low $\Delta T$ powerplant temperature on estuarine invertebrates. *J. Water Pollut. Control Fed.*, **48**, 2259–72.

Coutant, C. C. (1973). Effects of thermal shock on vulnerability of juvenile salmonids to predation. *J. Fish. Res. Board Can.*, **30**, 965–73.

Coutant, C. C., Ducharme, H. M., Jr. & Fisher, J. R. (1974). Effects of cold shock on juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation. *J. Fish. Res. Board Can.*, **31**, 351–4.

Doudoroff, P. (1942). The resistance and acclimatization of marine fishes to temperature changes. I. Experiments with *Girella nigricans* (Ayres). *Biol. Bull.* (Woods Hole), **83**, 219–44.

Farr, J. A. (1977). Impairment of antipredator behavior in *Palaemonetes pugio* by exposure to sublethal doses of parathion. *Trans. Am. Fish. Soc.*, **106**, 287–90.

Hayes, F. R., Pelluet, D. & Gorham, E. (1953). Some effects of temperature on the embryonic development of salmon (*Salmo salar*), *Can. J. Zool.*, **31**, 42–51.

Horst, T. S. (1975). The assessment of impact due to entrainment of ichthyoplankton. In *Fisheries and Energy Production: A Symposium.* ed. S. B. Saila, Heath Publishing Company, Lexington, Massachusetts, pp. 107–18.

Hoss, D. E., Clements, L. C. & Colby, D. R. (1977). Synergistic effects of exposure to temperature and chlorine on survival of young-of-the-year estuarine fishes. In *Physiological Responses of Marine Biota to Pollutants.* Academic Press, New York, pp. 345–55.

Hoss, D. E., Hettler, W. F., Jr. & Coston, L. C. (1974). Effects of thermal shock on larval estuarine fish—ecological implications with respect to entrainment in power plant cooling system. In *Early Life History of Fish.* ed. J. H. S. Blaxter, Springer-Verlag, New York, pp. 357–71.

Hoss, D. E., Peters, D. S. & Hettler, W. F., Jr. (1986). Effects of lowered water temperature on the survival and behavior of juvenile French grunt, *Haemulon flavolineatum. Bull. Mar. Sci.*, **39**, 134–8.

Hunter, J. R. (1976). Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. *NOAA Tech. Rep. NMFS Circ.*, **395**.

Hunter, J. R. (1981). Feeding ecology/predation. In *Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries.* ed R. Lasker, Washington Sea Grant Program, Seattle, pp. 34–77.

Hunter, J. R., Taylor, J. H. & Moser, H. G. (1979). Effect of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and Pacific mackerel, *Scomber japonicus*, during the embryonic stage. *Photochem. Photobiol.*, **27**, 1–14.

Koo, T. S. Y. & Johnson, M. L. (1978). Larval deformity in striped bass, *Morone saxatilis* (Walbaum) and blue back herring *Alosa aestivalis* (Mitchill) due to heat shock treatment of developing eggs. *Environ. Pollut.*, **16**, 137–49.

Lasker, R. (1964). An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. *Copeia*, **1964**, 399–405.

Longwell, A. C. & Hughes, J. B. (1981). Cytologic, cytogenetic, and embryonic state of Atlantic mackerel eggs from surface waters of the New York Bight in relation to pollution. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **178**, 76–8.

Matsumoto, W. M. (1984). Potential impact of ocean thermal energy conversion (OTEC) operation on fisheries. National Marine Fisheries Service, NOAA, Honolulu, Hawaii. *Southwest Fisheries Center Administrative Report H-84-4*, 29 pp.

May, R. C. (1974). Effects of temperature and salinity on yolk utilization in *Bairdiella icistia* (Jordan and Gilbert) (Pisces: Sciaenidae). *J. Exp. Mar. Biol. Ecol.*, **16**, 213–25.

Mazeaud, M. M., Mazeaud, F. & Donaldson, E. M. (1977). Primary and secondary effects of stress in fish: Some new data with a general review. *Trans. Am. Fish. Soc.*, **106**, 201–12.

Medvick, P. A. & Miller, J. M. (1979). Behavioral thermoregulation in three Hawaiian reef fishes. *Environ. Biol. Fishes*, **4**, 23–8.

Myers, E. P., Hoss, D. E., Matsumoto, W. M., Peters, D. S., Seki, M. P., Uchida, R. N., Ditmars, J. D. & Paddock, R. A. (1986). The potential impact of ocean thermal energy conversion (OTEC) on fisheries. *NOAA Tech. Rep. NMFS*, **40**.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. (1975). *Statistical Package for the Social Sciences.* (2nd edn), McGraw Hill, New York, 675 pp.

Norris, K. S. (1963). The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). *Ecol. Monogr.*, **33**, 23–62.

Ocean Thermal Corporation. (OTC) (1983). Ocean Thermal Energy Conversion (OTEC) site specific environmental assessment. Document No. L3 submitted to Department of Energy under Contract No. DE-AC01-82CE30716. Ocean Thermal Corporation, New York (Draft).

Oppenheimer, J. M. (1937). The normal stages of *Fundulus heteroclitus. Anat. Rec.*, **68**, 1–15.

Palko, B. J., Beardsley, G. L. & Richards, W. J. (1982). Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. *NOAA Tech. Rep. NMFS Circ.*, **443**. *FAO Fish. Biol. Synop.* **130**.

Pilati, D. A. (1976). Cold shock: Biological implications and a method for approximating transient environmental temperatures in the near-field region of a thermal discharge. *Sci. Tot. Environ.*, **6**, 227–37.

Rosenthal, H. & Alderdice, D. E. (1976). Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae. *J. Fish. Res. Board Can.*, **33**, 2047–65.

Saila, S. B. (ed). (1975). Fisheries and energy production. Heath Publishing Company, Lexington, Massachusetts, 300 pp.

Schubel, J. R. (1975). Some comments on the thermal effects of power plants on fish eggs and larvae. In *Fisheries and Energy Production.* ed S. B. Saila, Heath Publishing Company, Lexington, Massachusetts, pp. 31–54.

Schubel, J. R., Coutant, C. C. & Woodhead, P. M. J. (1978). Thermal effects of entrainment. In *Power Plant Entrainment: A Biological Assessment.* ed J. R. Schubel & B. C. Marcy, Academic Press, New York, pp. 19–73.

Shimada, S., Egami, N. & Shima, A. (1985). Comparison of cold, heat, and radiation sensitivities of the fish embryos among the genus Oryzias. *Comp. Bioch. Physiol.*, **82A**, 815–8.

Smith, C. F., Schubel, J. R., Greges, M. P., Itzkowitz, N., DiPiero, S. J., Longo, J. & Morgan, M. A. (1979). Thermal resistance characteristics of early life history stages of finfish from Long Island waters. *Mar. Sci. Res. Cent. Spec. Rep.* (Stony Brook), **26**, 79–9.

Talmage, S. S. & Coutant, C. C. (1979). Thermal effects. *J. Water Pollut. Control Fed.*, **51**, 1517–54.

Van Winkle, W. (Ed.). (1977). *Assessing the Effects of Powerplant Induced Mortalities of Fish Populations.* Pergamon Press, New York, 380 pp.

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# FOOD CHAINS AND FISHERIES: AN ASSESSMENT AFTER 20 YEARS

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**ABSTRACT.** Oceanic food chain research has been notably unsuccessful in predicting fish yield, chiefly because of inadequate methods for determining primary production and for the lack of data on transfer efficiencies between steps in food chains. Methods have improved in recent years in assessing primary production (both recycled and new) but the state of the science does not yet permit grand means of primary production to be assigned to the world's oceans nor for them to be used to predict fisheries yield.

## 1. INTRODUCTION

Almost 20 years ago, at the 1968 symposium on marine food chains (Steele, 1970) I presented data to show that it was impossible to maintain the 1932-33 population of sardines of about 3,000,000 metric tons (mtons) in the California Current with the primary production measured for the California Current and inshore waters where the sardine resides (Lasker, 1970). My data source for primary production was the late John D.H. Strickland who provided me with his most up-to-date estimate ($1 gC/m^2$ per day) of primary production for the area where sardines were found. These data were subsequently published (Eppley *et al.*, 1970). Sardines are zooplankton feeders and therefore they were at the top of a two step food chain. I used a conversion efficiency of 10% between steps in the food chain.

In the final analysis, there was no accounting for sustaining the large biomass with the primary production measured in the sardine's habitat. At that time I speculated that the sardine biomass may have been estimated at too high a level, or the estimates for primary and secondary production were too low.

Food chain research has contributed more to the knowledge of biogeochemical cycles in the ocean and to describing the driving forces behind the sinking flux of biogenic particles than to fisheries science in recent years. Primary production may not be the most important environmental variable for fish stocks. This is suggested by poor correlations between primary production and fish biomass and the fact that aggregations of food rather than total integrated food may

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be more important to larval fish survival (Lasker, 1975). Nevertheless at some level there must be a reckoning between the energy requirements of fish and the production of their food.

In this paper I reexamine this problem in light of the latest data available, examine other biological systems and try to come to some conclusion whether Food Chain Research has made a contribution to Fisheries Science.

## 2. THE PRIMARY PRODUCTION CONTROVERSY

For some time there has been general unhappiness among biological oceanographers with the Carbon-14 method of primary productivity measurements (Peterson, 1980). Studies of oxygen distribution in the north Pacific by Shulenberger and Reid (1981) have also cast doubt on previous work done in the "deserts of the sea" on primary production. They suggested that measurements of oxygen trapped below the surface layers of nutrient-poor oligotrophic regions, were evidence of an amount of primary production, heretofore not measured, and two to four times as much as ever reported for these areas throughout the world. Jenkins (1982) and Jenkins and Goldman (1985) came to similar conclusions based upon oxygen distributions in the north Atlantic. Recent measurements on the $CO_2$ system also seem to support the concept of extra oxygen production and unmeasured primary production (Brewer, *et al*. 1986, and Pers. Comm.).

Notwithstanding the argument by Platt (1984) and Platt and Harrison (1986) who see errors in interpretation and magnitude in the subsurface oxygen hypothesis, the ocean science community may have been underestimating primary production by some multiple in the open ocean (Kerr, 1983) and by some smaller fraction in inshore waters.

Toxicity of samplers and incubation bottles has been implicated in depressing the amount of carbon incorporation in the carbon-14 technique (Fitzwater *et al*., 1982). The trace metal "clean" methods of these authors appear to have resolved much of the problem and have been used in recent U.S. National Science Foundation programs aimed at improving primary production measurements.

## 3. RYTHER'S 1966 PAPER ON FISH PRODUCTION

The paper by Ryther (1966) is a good example of the extent to which primary production figures have been used in calculations on fish yield. Ryther divided the world's oceans into open ocean, coastal, and upwelling regions, then assigned 5, 3 and 1.5 trophic levels and 10, 15 and 20% efficiencies of transfer respectively, leading to the production of fish.

Based on productivity figures compiled and published by Russian scientists (Koblentz-Mishke, *et al*. 1970; this was In Press in 1969) and Steemann Nielsen and Jensen, (1957) using the Steemann Nielsen (1957) technique of Carbon-14 incorporation into phytoplankton, Ryther deduced that primary production would be at its maximum at $20 \times 10^9$

mtons of carbon per year in the world and that the world fish production can be only about 24 x $10^7$ mtons (wet weight) per year. From this figure he concluded that the world's commercial fish maximum sustainable yield could not exceed 10 x $10^7$ mtons per year.

Fishery biologists were quick to dispute Ryther's conclusions but chiefly his low estimate of what tropical oceans can produce in fish. Alverson *et al.* (1970) argued with Ryther's conclusion that 90% of the ocean is a "biological desert." They pointed out that it did not square with the fact that the yield in tunas, billfishes and other open ocean pelagic fishes in the mid 1960s was 2.5 to 3 x$10^6$ mtons annually, as against Ryther's estimate of only 1.6 x $10^6$ mtons per year total fish production. The tuna and billfish catch alone exceeded 2.2 x $10^6$ mtons in 1984, the last year for which statistics were compiled (FAO, 1986). To make their case, Alverson *et al.* (1970) included "tuna-like" fishes, many of which occur in coastal and upwelling regions, although they argued that it made no difference to their case.

In fairness to Ryther, he made the conservative assumption that there are most likely 5 steps in the food chain in the open ocean, as opposed to about 1.5 in upwelling systems, and used a reasonable 10% efficiency in energy transfer between steps in the open ocean. The four to five step food chain has been verified by Mearns *et al.*(1981) and Rau *et al.* (1983). The important point to be made however is that Ryther calculated a maximum sustainable yield for fisheries for all the world's oceans of 100 million mtons. This maximum was the major point of contention from fishery scientists. Alverson *et al.* (1980) were convinced this was too low. A recent paper by Wise (1984) makes the point that 100-120 million mtons limitation may only be due to fishing practices and consumer acceptance. He leaves his readers with the impression that all previous prognostications of status quo for world fisheries (*e.g.* United States, 1980) have been mistaken and will continue to underestimate harvests from the sea. We have very reliable statistics on the world marine fish catch which show that the tuna and billfish catch has been increasing since 1968 by 70000 mtons per year and for all marine fish by 1.5 x $10^6$ mtons per year for the last 35 years (FAO, 1986) and this has been one of the causes for the optimism of fishery scientists.

A recent estimate of primary production for the global ocean is 51 x $10^9$ mtons of carbon per year (Martin *et al.*, 1987). The mean productivity rates for the open ocean, coastal zone and upwelling areas of Martin *et al.* exceed those summarized by Ryther (1969) by factors of 2.6, 2.5 and 1.4 respectively. All but about 7 x $10^9$ mtons of this production is recycled in the upper 100 m by processes including fish metabolism. The fish catch itself is an export from the productive system of the surface ocean and thus cannot exceed global "new production" (Dugdale and Goering, 1967). Global new production is probably about 20% of the total. A recent estimate of new production in the equatorial Pacific alone is 1 x $10^9$ mtons per year (Chavez and Barber, 1987). Global new production is well in excess of the fish catch but the fate of most of this new production is to end up as biogenic particles in the depths of the sea (Eppley and Peterson, biogenic particles in the depths of the sea (Eppley and Peterson, 1979).

The uncertainties of Ryther's educated assumptions and the importance of correct figures in predicting the world fish catch have been an impetus to food chain scientists to make the pertinent measurements more accurate and therefore to obtain more reliable production values for the world's oceans. Should the fishing community view the future with unbridled optimism or is the leveling off of world fisheries just a matter of a few years' time?

## 4. WHAT CARBON INCORPORATION FIGURES TO USE?

For the coastal Pacific sardine, (*Sardinops sagax = S. caeruleus*), we have population figures from California and Baja California fishery data (Murphy, 1966 and MacCall, 1979). At its maximum, in 1932-33, the subpopulation centered in the Southern California Bight was 3.2 million mtons. The energy required for respiration by this population was $2.8 \times 10^{12}$Kcal/month, and the population required an intake of $2.2 \times 10^{11}$g C/month (Lasker, 1970).

The area covered by this population was $4.14 \times 10^{10}m^2$. At $1g/m^2C$ produced for a 30 day month, the primary production for this area is calculated to be $1.24 \times 10^{12}$gC/month.

| | | |
|---|---|---|
| Primary production. | 1.24 x | $10^{12}$gC/month |
| Zooplankton production. | 0.124 | " |
| Sardine respiration. | 0.22 | " |

These results are not substantially different from what I reported in 1970. Ryther used a 20% efficiency figure between phyto- and zooplankton while I used 10%. On the other hand I used $1gC/m^2$ per day as a best estimate of coastal productivity and now the figure, derived from many more Carbon-14 measurements, is best put at 0.5g $C/m^2$ per day for the inner Southern California Bight (Smith and Eppley, 1982) while higher values are found offshore in the California Current (Hayward and Venrick, 1984). When the Ryther and Smith and Eppley figures are used, the calculation is:

| | | |
|---|---|---|
| Primary Production. | 0.62 x | $10^{12}$gC/month |
| Zooplankton production. | 0.12 | " |
| Sardine Respiration. | 0.22 | " |

Despite the 2X discrepancy between calculated zooplankton production and the amount of carbon needed to support the 3 million mtons of sardines, the figures are as good as we can expect given the present state of knowledge of primary production and transfer efficiency in the coastal zone, the lack of information on secondary production, and the errors in fish population estimation. For example, is estimating the sardine population, Murphy (1966) used an assumed natural mortality (M) figure of 0.5. Had he used 0.4 the estimated biomass would have been about 20% higher.

It also seems likely that to the north, off central and northern California, the highly energetic "jets and squirts" which move large quantities of cold, nutrient-enriched water offshore and become entrained into the southward moving California current (Lasker, *et al.*, 1981; Treganza *et al.*, 1987) add more primary production to the habitat of the sardine than has been included in the gross overall average. For the sardine and other fauna of this region it seems that we have achieved about the best input-output balance for the population if we agree that there are still uncertainties in our understanding of transfer efficiencies and in the methods and time scales of sampling used to measure primary production, and that there are probably nutrient inputs not yet accounted for. A promise of satellite technology is that we may acquire in the future much more comprehensive information on phytoplankton production on synoptic scales (Eppley *et al.* 1985).

## 5. OTHER UPWELLING SYSTEMS

While the northern and central parts of the California coast are areas of intense upwelling, with the production of jets and squirts bringing in as yet unmeasured quantities of nutrients, the Peruvian upwelling system by contrast supports much greater populations of fish, particularly the Peruvian anchoveta, *Engraulis ringens* and the Chilean sardine, *Sardinops sagax*. At its height the spawning biomass of the Peruvian anchoveta exceeded 20 million mtons (Csirke, 1980; Tsukayama, 1982) and the catch alone in 1968 was greater than 12 million mtons. The anchoveta is a phytoplankton feeder and the one-step food chain undoubtedly helped make this remarkable upwelling system more productive of fish. A 20 million ton anchoveta population has a carbon intake rate of approximately 6.8 x $10^{13}$gC/yr based on the respiration measurements of Villavicencio (1981) where the Peruvian anchoveta has a total metabolic requirement of 87.2 cal./g per day. The conversion of calories to carbon is based on the combustion of glucose where 1g C yields 9350 calories. Chavez and Barber (1987) conclude from their study that 1409gC/$m^2$ per year are produced in the Peruvian upwelling zone (3.84gC/$m^2$ per day) and that the area of that zone is 1.82 x 1011 $m^2$. The total production was calculated to be 2.6 x $10^{14}$gC per year, 40 times more than required by a 20 million ton anchoveta population. These exercises serve to illustrate that, at least in upwelling areas, the correspondence between carbon production measured and that needed by large fish populations is within reasonable bounds. Whether the discrepancies are due to primary production measurements or the area to which they are applied, other inaccuracies, *e.g.* estimating the biomass of large fish populations, the utilization of phytoplankton by other organisms, or extrapolation of laboratory oxygen consumption figures to caloric needs of field populations, cannot be stated at this time, and indeed these may be unanswerable questions.

## 6. FISH POPULATIONS IN "OLIGOTROPHIC" SEAS

Olson and Boggs (1986) have produced a significant work in their study of the apex predator, *Thunnus albacares*, the yellowfin tuna of the eastern tropical Pacific Ocean. This species is abundant throughout the world's tropical seas and may typify the abundances of the major apex predators in the open ocean. Sharp and Francis (1976) estimated an unexploited population of about 600,000 mtons was required to support the yellowfin surface fishery of 1966-71. Olson and Boggs used a 300,000 mton estimate for 1970-72 standing stocks, which was calculated by Inter-American Tropical Tuna Commission scientists (Anon, 1986) to calculate predation rates of the population. By using the more conservative figure of 300,000 mtons, an annual consumption of $4.5 \times 10^9$kg of forage ($\sim 1.24 \times 10^{12}$gC) and 5 steps in the food chain (Mearns *et al.*, 1981; Rau *et al.* 1983) with an efficiency between steps of 10%, we find that for the area of the yellowfin tuna habitat, $1.7 \times 10^{13}$ m$^2$, 730gC/m$^2$ primary production per year are needed or approximately 2gC/m$^2$ per day over the whole area. This has to be an underestimate since no other top predators are included in the biomass. The most recent (1985) biomass estimate for yellowfin tuna in this area is 450,000 mtons, the result of a post-El Niño succession of three exceptional year classes (Anon. 1986).

Feldman (1986) has shown that the productive area of the eastern tropical Pacific has varied an order of magnitude between years based on satellite chlorophyll images. Dandonneau (this volume) using extensive ship-of-opportunity data, confirmed and extended these observations to the southwestern tropical Pacific and suggested a mechanism for this increased production. Cooling of the surface layer in the winter increases the depth of the mixed layer which overturns and brings up nitrate from the deep.

Owen and Zeitschel (1970) showed a seasonal change in primary production for this region using the Carbon-14 method, from 127 mg/m$^2$ per day to 318 mg/m$^2$ per day, or an average annual production of 75g/m$^2$, an order of magnitude lower than needed by this population of yellowfin tuna as calculated using the 10% transfer efficiency and the excellent data on forage requirements by Olson and Boggs (1986), but slightly more than the rate used by Ryther (50g C/m$^2$ per year) to make his calculations.

Between 90° and 180°W in the equatorial tropical Pacific is an oceanic upwelling zone which is unusually productive for open ocean areas. Ryther (1969) included areas like this in the estimate of 100gC/m$^2$ per year for the coastal zone (but not upwelling zone) production. Chavez and Barber (1987) suggest that the oceanographic upwelling zone of the tropical Pacific produces about 197gC/m$^2$ per year, about twice what Ryther estimated. While not an order of magnitude higher, the vast area over which this production occurs leads to the conclusion that populations in nearby areas, such as the yellowfin tuna in the eastern tropical Pacific, must benefit from this production.

Another possible mechanism for enhancing production in oligotrophic areas is nitrogen fixation. Blue-green algae in tropical seas have been estimated to fix 5 x $10^6$ mtons annually (Carpenter, 1983). It is difficult to put this figure in perspective because of the uncertainty of the amount of total new nitrogen available in tropical seas.

## 7. CONCLUSIONS

Marine food chain research seems still to be in its infancy when it comes to energy budgets. The numbers being generated for primary production are constantly being upgraded and the trend has been toward substantial increases for all areas of the world's oceans. Other new findings also increase the values to be used in calculations of ocean productivity. These are 1) the determination of markedly increased production by equatorial upwelling areas as well as the size of those areas (Chavez and Barber, 1987), 2) nutrient enrichment by jets and squirts of the coastal zone, 3) nutrient enrichment by eddy entrainment (Simpson, 1986), 4) nutrient enrichment by deepening and overturning the mixed layer in tropical seas (Dandonneau, 1987), 5) the possibility of a utilizable pool of dissolved organic nitrogen in "oligotrophic" seas (Suzuki *et al.*, 1985), 6) the continuing technical improvements in the methods for determining primary production, and 7) new methods for the more accurate determination of fish biomass (Lasker, 1985).

Other problems, not very different than those discussed 20 years ago, will also have to be resolved. For example, too few data on secondary production and percent transfer of energy through steps in the food chain prevent the determination of grand means for different ocean regimes. We lack too the information on feedback mechanisms in food chains which may influence transfer efficiencies.

All of these points bring us to the obvious conclusion that ocean scientists are not yet in a position to determine what the yield of food from the sea will be for the foreseeable future. The exercises to do so thus far have been important in pointing out the major problems in determining the starting point (primary production) and where we end up (commercial fisheries). A conference of this kind in 10 years may be able to resolve some of these issues, but we cannot do it today.

## 8. ACKNOWLEDGEMENTS

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## 9. REFERENCES

Alverson, D.L., A.R. Longhurst and J.A. Gulland: 1970, 'How much food from the sea?', *Science* **168**, 503-505.

Anon: 1986, *Annual Report of the Inter-American Tropical* Tuna Commission, La Jolla, California, U.S.A., 248 p.

Brewer, P.G., K.W. Bruland, R.W. Eppley and J.J. McCarthy: 1986, 'The Global Ocean Flux Study (GOFS): Status of the U.S. GOFS Program', *Eos* **67**, 827-832.

Carpenter, E.J.: 1983, 'Nitrogen fixation by marine Oscillatoria (Trichodesmium) in the world's oceans', in E.J. Carpenter and D.G. Capone (eds.), *Nitrogen in the Marine Environment*, Academic Press, New York, p.65-103.

Chavez, F.P. and R.T. Barber: 1967, 'An estimate of new production in the equatorial Pacific', *Deep-Sea Res.* In Press.

Dandonneau, Y.: 1988, 'Seasonal or aperiodic cessation of oligotrophy in the tropical Pacific Ocean', in B.J. Rothschild (ed.), *Toward a Theory on Biological-Physical Interaction in the World Ocean*, Kluwer Academic Publishers, Dordrecht, pp. 137–156.

Dugdale, R.C. and J.J. Goering: 1967, 'Uptake of new and regenerate forms of nitrogen in primary productivity', *Limnol. Oceanogr.* **12**, 196-206.

Eppley, R.W. and B.J. Peterson: 1979, 'Particulate organic matter flux and planktonic new production in the deep ocean', *Nature* **282**, 677-680.

Eppley, R.W., F.M.H. Reid and J.D.H. Strickland: 1970, 'Estimates of phytoplankton crop size, growth rate, and primary production', *Bull. Scripps Inst. Oceanogr.* **17**, 33-42.

Eppley, R.W., E. Stewart, M.R. Abbott and U. Heyman: 1985, 'Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight', *J. Plankton Res.* **7**, 57-70.

FAO: 1986, *Yearbook of fishery statistics: catches and landings*, 1984. 58, 451 p.

Feldman, G.C.: 1986, 'Variability of the productive habitat in the eastern equatorial Pacific', *Eos* **67**, 106-108.

Fitzwater, S.E., G.A. Knauer and J.H. Martin: 1982, 'Metal contamination and its effect on primary production measurements', *Limnol. Oceanogr.* **27**, 544-551.

Hayward, T.L. and E.L. Venrick: 1982, 'Relation between surface chlorophyll, integrated chlorophyll and integrated primary production', *Mar. Biol.* **69**, 247-252.

Jenkins, W.J. and J.C. Goldman: 1985, 'Seasonal oxygen cycling and primary production in the Sargasso Sea', *J. Mar. Res.* **43**, 465-491.

Kerr, R.A.: 1983, 'Are the ocean's deserts blooming?', *Science* **220**, 397-398.

Koblentz-Mishke, O.I., V.V. Volkovinsky and J.G. Kabanova: 1970, 'Plankton primary production of the world ocean', in *Scientific Exploration of the South Pacific*, National Academy of Sciences, Washington, D.C. p.183-193.

Lasker, R.: 1970, 'Utilization of zooplankton energy by a Pacific sardine population in the California current', in J.H. Steele (ed.), *Marine Food Chains*, Oliver and Boyd, Edinburgh, p. 265-284.

Lasker, R.: 1975, 'Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding', *Fish. Bull. (U.S.)* 73, 453-462.

Lasker, R., J. Pelaez and R.M. Laurs: 1981, 'The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (Engraulis mordax)', *Remote Sensing of Environment* 11, 439-453.

Lasker, R. (ed.): 1985, 'An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*', *NOAA Technical Rep. NMFS* 36, 99p.

MacCall, A.D.: 1979, 'Population estimates for the waning years of the Pacific sardine fishery', *Calif. Coop. Oceanic. Fish. Invest. Rep.* 20, 72-82.

Martin, J.H., G.A. Knauer, D.M. Karl and W.W. Broenkow: 1987, 'VERTEX: Carbon cycling in the northeast Pacific', *Deep-Sea Res.* 34, 267-285.

Mearns, A.J., D.R. Young, R.J. Olson, and H.A. Schafer: 1981, 'Trophic structure and the cesium-potassium ratio in pelagic ecosystems', *Calif. Coop. Oceanic Fish. Invest. Rep.* 22, 99-110.

Murphy, G.I.: 1966, 'Population biology of the Pacific sardine (*Sardinops caerulea)*', *Proceedings Calif. Acad. Sci.* 34, 1-84.

Olson, R.J. and C.H. Boggs: 1986, 'Apex predation by yellowfin tuna (Thunnus albacares): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations', *Can. J. Fish. Aquat. Sci.* 43, 1760-1775.

Owen, R.W. and B. Zeitzschel: 1970, 'Phytoplankton production: seasonal change in the oceanic eastern tropical Pacific, *Mar. Biol.* 7, 32-36.

Peterson, B.J.: 1980, 'Aquatic primary productivity and the $^{14}C$-$CO_2$ method: a history of the productivity problem', *Ann. Rev. Ecol. System* 11, 359-385.

Platt, T.: 1984, 'Primary productivity in the central North Pacific: comparison to oxygen and carbon fluxes', *Deep-Sea Res.* 31, 1311-1319.

Platt, T. and W.G. Harrison: 1986, 'Reconciliation of carbon and oxygen fluxes in the upper ocean', *Deep-Sea Res.* 33, 273-276.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olson, H.A. Schafer, and I.R. Kaplan: 1983, 'Animal $^{13}C/^{12}$ correlates with trophic level in pelagic food webs', *Ecology* 64, 1314-1318.

Ryther, J.H.: 1969, 'Photosynthesis and fish production in the sea.' *Science* 166, 72-76.

Shulenberger, E. and J.L. Reid: 1981, 'The Pacific shallow oxygen maximum, deep chlorophyll maximum, and primary productivity, reconsidered', *Deep-Sea Res.* 28, 901-919.

Simpson, J.J.: 1986, 'Processes affecting upper ocean chemical structure in an eastern boundary current', in J.D. Burton, P.G. Brewer and R. Chesselet (eds.), *Dynamic Processes in the Chemistry of the Upper Ocean*, Plenum Publ. Corp, p.53-77.

Smith, P.E. and R.W. Eppley: 1982, 'Primary production and the anchovy population in the Southern California Bight: Comparison of time series', *Limnol. Oceanogr.* 27, 1-17.

Steele, J.H. (ed.): 1970, *Marine Food Chains*, Oliver and Boyd, Edinburgh, 552 p.

Steemann Nielsen, E.: 1952, 'The use of radio-active carbon ($C^{14}$) for measuring organic production in the sea', *J. Cons. Perm. Int. Explor. Mer* **18**, 117-140.

Steemann Nielsen, E. and E.A. Jensen: 1957, 'Primary oceanic production. The autotrophic production of organic matter in the oceans', *Galathea Report* **1**, 49-136.

Suzuki, Y., Y. Sugimura and T. Itoh: 1985, 'A catalytic oxidation method for the determination of total nitrogen dissolved in seawater', *Mar. Chem.* **16**, 83-97.

Thomas, W.H., E.H. Renger and A.N. Dotson: 1971, 'Near-surface organic nitrogen in the eastern tropical Pacific ocean', *Deep-Sea Res.* **18**, 63-71.

Treganza, E.D., D.G. Redalje and R.W. Garwood: 1987, 'Chemical flux, mixed layer entrainment and phytoplankton blooms at upwelling fronts in the California coastal zone', *Continental Shelf Res.* 7, 89-105.

United States. Council on Environmental Quality: 1980, *The Global 2000 Report to the President: Entering the Twenty-First Century*, Vol. 2, Technical Report, G.O. Barney, Study Director, Washington, D.C., Government Printing Office, 766p.

Villavicencio R.Z.: 1981, 'Investigacion preliminar de los requerimientos energeticos de anchoveta adulta (metabolismo estandar y actividad)', *Bol. Inst. del Mar del Peru*, Volumen Extraordinario, p. 193-205.

Wise, John P.: 1984, 'The future of food from the sea', in J.L. Simon and H. Kahn (eds.), *The Resourceful Earth, a response to Global 2000*, Basil Blackwell Publ. Oxford and New York, p. 113-127.

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# I-3. Studies on the Northern Anchovy; Biology, Recruitment and Fishery Oceanography

Reuben LASKER*

I would like to thank the Japanese Society of Fisheries Oceanography for this invitation to address the Society on the main subject studied in my laboratory, fishery oceanography of the Northern anchovy, *Engraulis mordax*. I am delighted to be in Japan and to have this opportunity to meet with my esteemed Japanese colleagues.

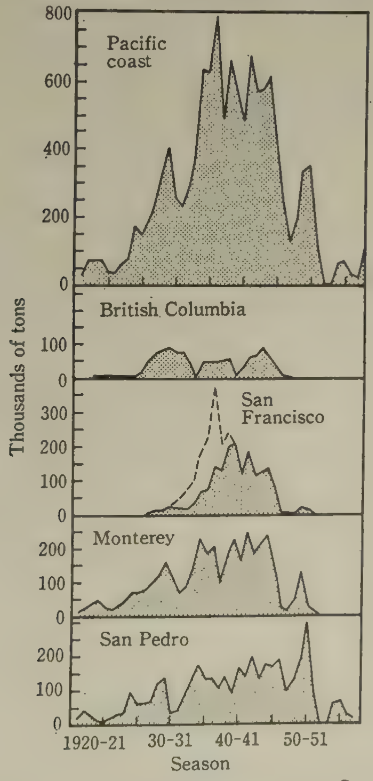

Fig. 1. Catch of the Pacific sardine, *Sardinops sagax*=*S. caerulea*, off California. The dotted line refers to catch processed in offshore floating canneries (after Marr, 1960).

**Introduction**

Before I discuss our work on the northern anchovy, I will describe briefly the events which led to our involvement in the study of sardines and anchovies. In 1949 a crisis occurred in the rich fishery for the Pacific sardine, *Sardinops sagax* off California. Catches fell off precipitously and the huge losses suffered by the fishermen and canners resulted in an extreme economic depression on Monterey's Cannery Row and elsewhere in the state of California. A graph of the sardine catch off the Pacific west coast from Canada to California is shown in Fig. 1.

The up-and-down nature of clupeoid catches is well-known throughout the world. The Peruvian anchoveta (Fig. 2) supported the largest fishery in the world in 1970, more than 12 million tons, and the collapse of that fishery also caused enormous economic hardship. Today the price of fish meal ($280/mt in the U.S.) is very low because the traditional market for fish meal, the poultry and

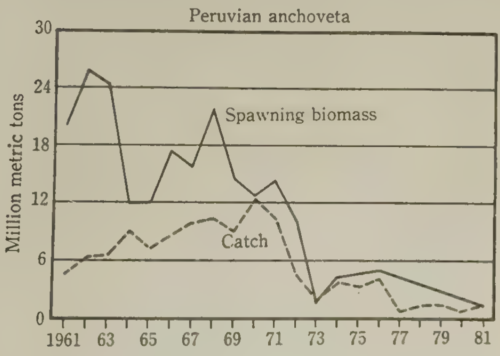

Fig. 2. Spawning biomass and catch of the Peruvian anchoveta, *Engraulis ringens* (after Tsukayama, 1982).

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cattle food manufacturers, switched to soybeans during the anchoveta's collapse and fish meal has never fully recovered its market, even after 14 years.

Another good example of the crash of a clupeoid population is that of the Japanese sardine, *Sardinops melanosticta* (Fig.3). This illustrates another phenomenon of sardine and anchovy populations, the ability to recover from apparent catastrophe and to produce enormous catches. Among the clupeoids the capacity to rebound from extremely low population sizes has also been seen in recent

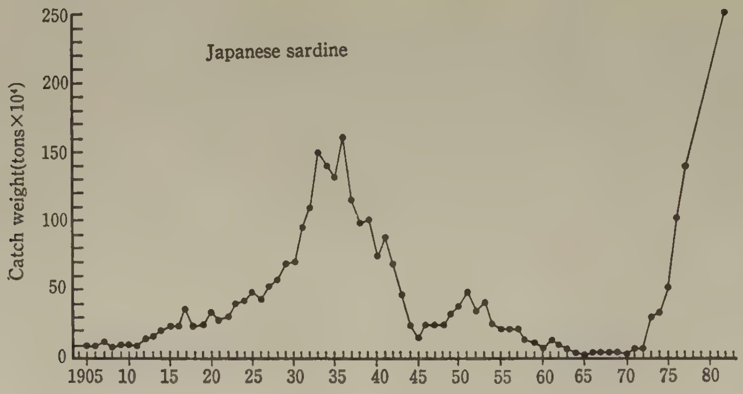

Fig. 3. Catch of the Japanese sardine, *Sardinops melanosticta* (after Kondo, 1980 and Tanaka, 1983).

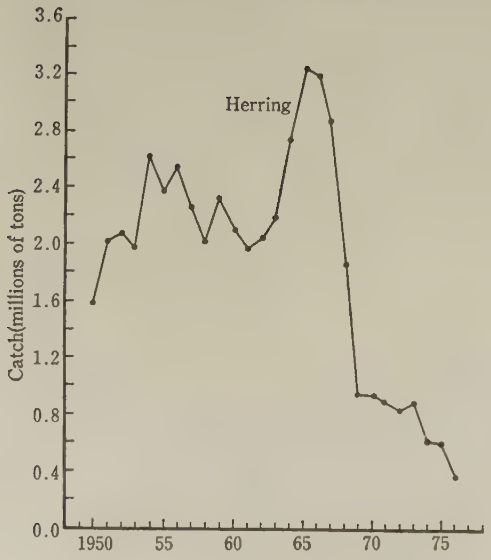

Fig. 4. Catch of the North Sea herring, *Clupea harengus* (after Schumacher, 1980).

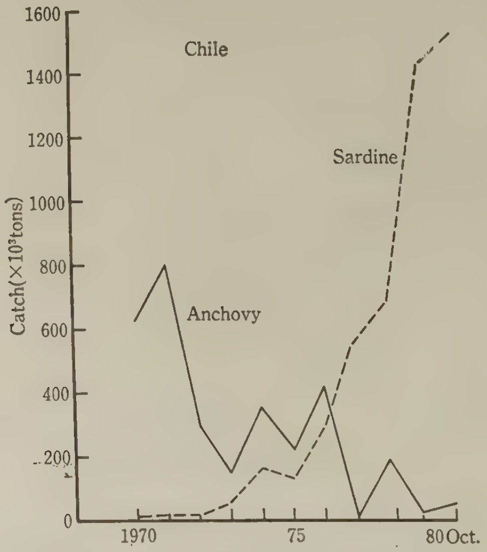

Fig. 5. Catch of the Peruvian anchoveta and the Chilean sardine by Chile(O. Rojas, Instituto de Fomento Pesquero, Santiago, Chile, Personal communication).

times in the Atlanto-Scandian herring (Fig. 4) and the Chilean sardine (Fig. 5). While this paper concerns clupeoids almost entirely, it should be understood that other fishes, such as the mackerels, cod and haddock also undergo similarly large fluctuations in population size.

The collapse of the sardine fishery off California was the major reason for the establishment of a U.S. Government research laboratory (now the Southwest Fisheries Center) to study the problem of fish population fluctuations. In the early 1950s a cooperative organization was set up in California which included the Southwest Fisheries Center, the Scripps Institution of Oceanography and the California Department of Fish and Game to find out what happened to the Pacific sardine. Today this organization is known as the California Cooperative Oceanic Fisheries Investigations, or CalCOFI. From the inception of the study, the scientists involved approached the problem from an *ecosystems* point of view. This meant that instead of just investigating the sardine, all the important fish of coastal California and the California Current were to be studied. The chief pioneer in these studies was Dr. Elbert H. Ahlstrom who began the unique surveys for ichthyoplankton off California and Mexico to answer the questions: 1) How is the sardine distributed? and 2) How is the population changing with time? From the first, one of the major hypotheses to be investigated was that year class strength may be determined environmentally (Sette, 1943).

While the sardine was disappearing from California waters, the northern anchovy was increasing in numbers. The fishery on sardines shifted to anchovies and the scientists also shifted their attention. We knew that both species ate the same kinds of food and that spawning overlapped in space and time. The anchovy was not new to us since studies on this species had been going on at the same time we were investigating the sardine, due to Dr. Ahlstrom's insistence on studying all the important fishes off California.

Because wide swings in population size are a relatively periodic and unusual property of clupeoid populations, these fishes serve as excellent subjects for studying the causes of recruitment success or failure.

### § 1. Is recruitment success of anchovies density dependent or density independent?

An examination of the events leading to the loss of the huge anchoveta fishery off Peru brought fishery experts to the conclusion that excessive fishing on the anchoveta parent stock reduced its reproductive potential below a level that could insure survival of a new year class and that fishing by man was the chief cause of recruitment failure (Murphy, 1974) but environmental effects were not ruled out (Fig. 6). In speculating about what happened to the Pacific sardine, Clark and Marr (1955), two of the scientists working on the California sardine program in the early 1950s, believed that there must be some minimum stock size to allow successful reproduction of the Pacific sardine although they could not say what the minimum was. Marr suggested that something in the environment caused the stock to be depressed below this minimum threshold level while Clark was certain that it was overfishing that prevented recovery of the population.

To a great extent this confusion exists today. The fishery biologist still has the task of trying to determine whether density dependent or density

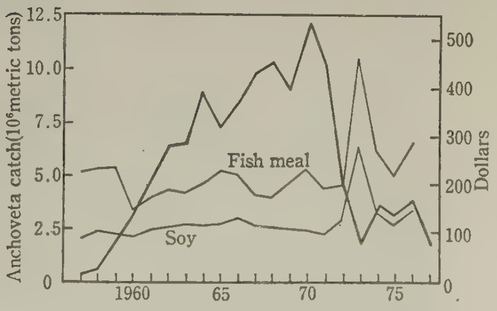

Fig. 6. Catch of the Peruvian anchoveta and the price of fish meal and soy beans from 1958 through 1977 (after Barber *et al.*, 1980).

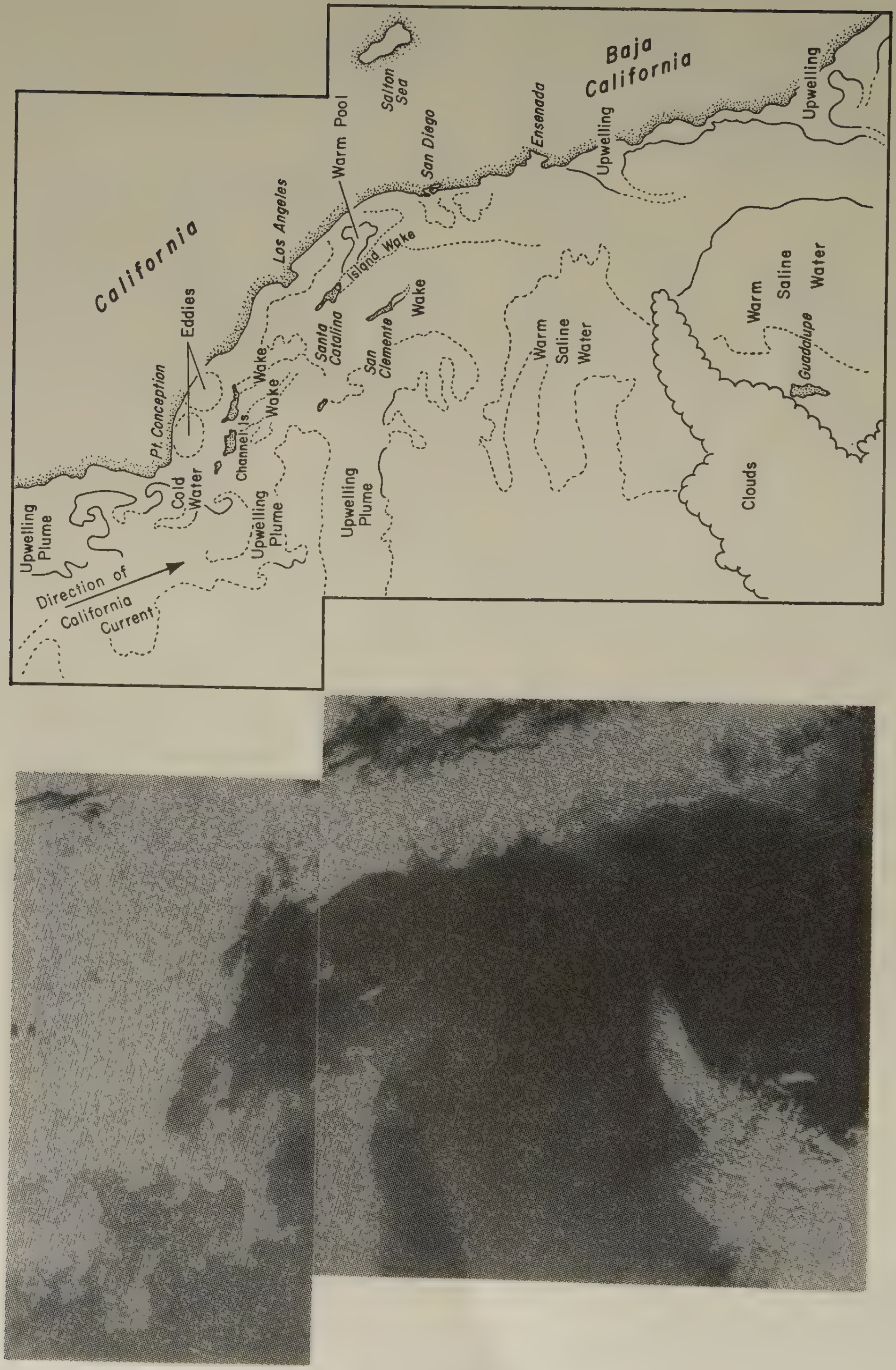
California
Pt. Conception
Eddies
Los Angeles
Warm Pool
Salton Sea
San Diego
Ensenada
Baja California
Upwelling
Upwelling
Island Wake
Santa Catalina
San Clemente
Wake
Wake
Wake
Channel Is.
Cold Water
Upwelling Plume
Upwelling Plume
Upwelling Plume
Direction of California Current
Warm Saline Water
Warm Saline Water
Guadalupe
Clouds

Fig. 7. Left panel: satellite image of sea surface temperatures, March 29, 1980, off the coast of California and Baja California; Right panel: line drawing indicating important oceanographic features seen in the satellite image (after Lasker *et al.* 1981).

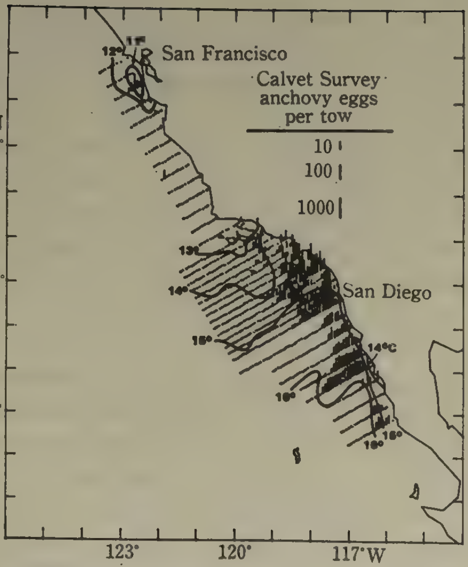
San Francisco
Calvet Survey anchovy eggs per tow
10
100
1000
San Diego
11°
12°
13°
14°
15°
16°
14°C
16°
16°
N
36°
33°
30°
123°
120°
117°W

Fig. 8. Distribution of anchovy spawning off California in February 1982 as related to sea surface temperature (after Picquelle and Hewitt, 1983).

independent factors, or both, determine year class strength. Density dependency suggests that the size of the spawning stock and the number of eggs spawned has a direct relationship to the number of recruits while density independency implies that the causes of stock fluctuation are mainly environmental.

## § 2. The California current and the Southern California Bight

The satellite picture of the nearshore ocean off California illustrates some general features of the oceanography of the California coastal zone (Fig. 7). About 150 km off the coast is the California Current which is part of the large-scale, anticyclonic North Pacific gyre. The northern anchovy and the Pacific sardine are coastal fish whose main habitat is the Southern California Bight. The whole California coast is an active upwelling region but the Southern California Bight acts as a refuge because the shoreline curves inward and

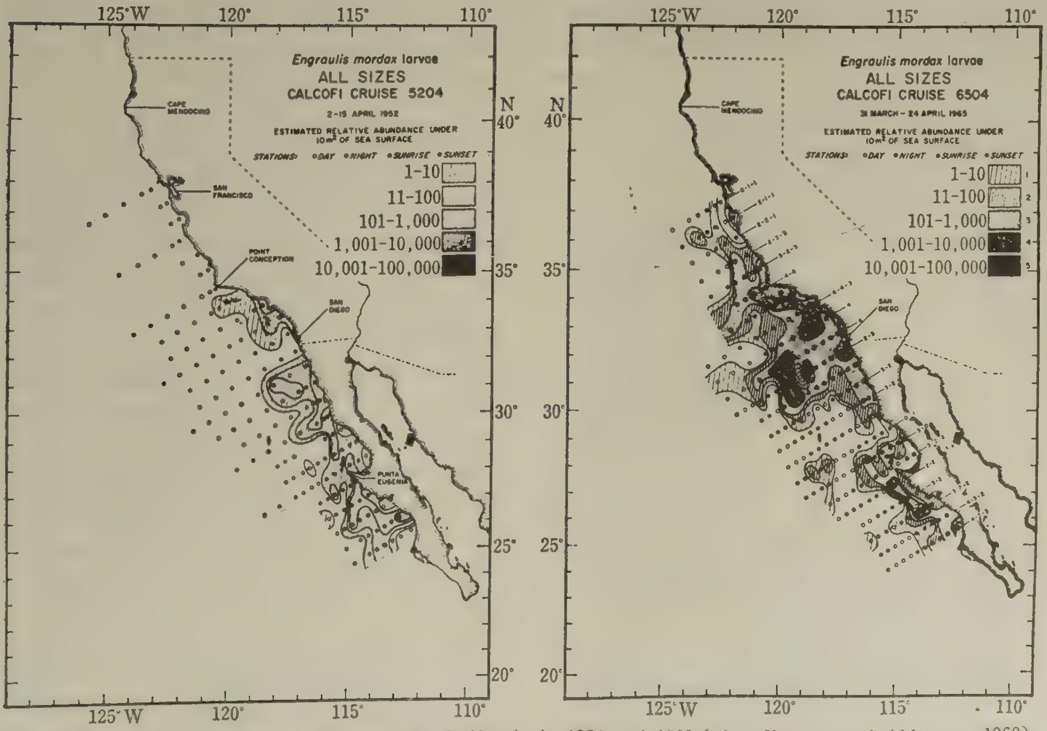
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 5204
2-15 APRIL 1952
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: DAY NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
Engraulis mordax larvae
ALL SIZES
CALCOFI CRUISE 6504
31 MARCH - 24 APRIL 1965
ESTIMATED RELATIVE ABUNDANCE UNDER 10m² OF SEA SURFACE
STATIONS: DAY NIGHT SUNRISE SUNSET
1-10
11-100
101-1,000
1,001-10,000
10,001-100,000
CAPE MENDOCINO
SAN DIEGO
125°W
120°
115°
110°
N
40°
35°
30°
25°
20°

Fig. 9. Distribution of anchovy larvae off California in 1954 and 1962 (after Kramer and Ahlstrom, 1968).

the Bight is protected by the Channel Islands (Fig. 8). A distribution map (Fig. 9) of anchovies illustrates how this species uses the Bight as its essential habitat and ranges beyond it when its population exceeds the carrying capacity of the near shore habitat.

## § 3. The paleosedimentary record

Soutar and Isaacs (1974) working at the Scripps Institution of Oceanography examined cores taken in the anaerobic Santa Barbara Basin which is in the Southern California Bight, for evidence of anchovies, sardines and hake. Varves, as those cores are called, contain undisturbed sediments, thousands of years old. Fish scales falling to the bottom of the ocean became trapped in these sediments and are found in layers which can be accurately dated. By examining each layer of sediment for fish scales an index of anchovy, sardine and hake populations could be constructed. Fig. 10 shows data taken from their paper which illustrates the relative magnitude of these fish populations from 1800 when no fishery of any size existed on these populations.

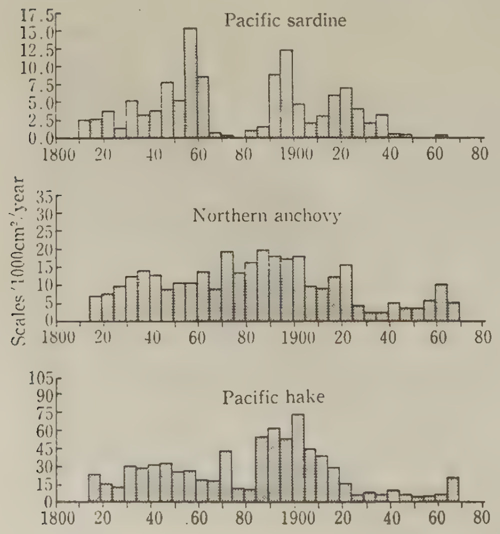

Fig. 10. The concentration of sardine, anchovy, and hake scales in anaerobic cores taken from the Santa Barbara Basin off California (modified after Soutar and Isaacs, 1974).

The results clearly show that the sardine and anchovy have fluctuated in population size even when no fishery was present. Exceptional sardine year classes occurred in 1855 and 1865 but this did not prevent the natural but sharp decline in the 1870s. The drastic decline in the 1940s which precipitated our investigations and was reflected in declining catches, was also seen in the Santa Barbara Basin varves.

## § 4. The Japanese sardine

*Sardinops melanosticta* is one of the more remarkable examples of the resiliency of the clupeoid's ability to recover if the conditions for survival are favorable. Resurgence from a virtuallhyunfishable level to the current level of a 4.2 million metric ton catch off Japan in 1984 has been recorded. Kondo (1980) has written that the 1972 year class probably had extraordinarily good conditions for larval survival because of a change in the course of the Kuroshio Current. The importance of this example is that it shows that even very small populations of clupeoids are able to have unusually successful recruitment.

## § 5. The northern anchovy

In common with other clupeoids the northern anchovy is highly fecund, and each female spawns from 20 to 30 times during a span of about 4 months, a spawning season which extends from December through April in California and Baja California coastal waters. This frequency of spawning was discovered by my colleagues Dr. John Hunter and Dr. Steve Goldberg (1980) and constitutes an important contribution to our knowledge of pelagic fishes. It afforded us an opportunity to investigate whether recruitment is density dependent based on the number of fish spawning and the number of eggs spawned or density independent mechanisms under environmental control.

## § 6. The first-feeding larva and the critical period

Johan Hjort (1913, 1926) while working on the

Atlanto-Scandian herring suggested that if newly hatched larvae did not find suitable food as soon as they were ready to eat then they would die. This required that there has to be simultaneous development of the special plants and nauplii used for food when the larvae were ready to eat. Hjort suggested this hypothesis because the early culture work of the French scientists Fabre-Domergue and Bietrix (1905) showed that sole larvae (*Solea vulgaris=S. solea*) started to look for food even before the yolk-sac was absorbed, and if they did not find it right away, the larvae became "anaemic" and died of starvation. To Hjort this laboratory observation suggested an explanation for the fact that occasionally there appeared coincident good year classes of several different species of fish in the Norwegian fisheries; that is, when good larval food is available, it feeds many species. The idea that there is one stage in the early life history of a species whose ability or inability to capture food can account for the success or failure of a year class has been called the "critical period" hypothesis.

The critical period hypothesis provided the motivation for research into the mortality and survival of anchovy larvae in La Jolla. However, early in our work we recognized that there were two possible processes involved in larval fish mortality, starvation and predation. I shall discuss each of these in relation to the anchovy.

## § 7. Experiments on mortality of first-feeding larvae

Our laboratory studies on the anchovy always indicated that the only way we could insure survival of *some* of the larvae, usually a very small percentage, was to provide food at very high densities. It seemed to us that this observation was incompatible with what we knew about the ocean. For example, we found that feeding and survival in the laboratory required about one nauplius per milliliter or 1000 per liter (O'Connell and Raymond, 1970) but the maximum found in California waters is only about 200 nauplii per liter (Beers and Stewart, 1967; Lasker, 1978). Other food organisms were found to support anchovy growth and survival but generally at even higher densities than nauplii. For example, the naked dinoflagellate *Gymnodinium splendens* was found to be good food at densities of about 30000 per liter or higher. The problem was to find where particles of the right size and in the right density occur in the ocean and to determine what affected their concentration and distribution. Once this was done, the intent was to predict from larval food availability whether larval survival would be good or bad and subsequently whether or not there would be a good year class.

## § 8. Effects of storms and upwellings

A simple bioassay for larval anchovy food was devised in 1974 (Lasker, 1975) by spawning and hatching anchovy larvae in the laboratory, taking the first-feeding larvae to sea in laboratory containers, and by putting the larvae in natural concentrations of food organisms taken from various depths in the anchovy's habitat. The finding was unexpected; food organisms of the right size and of the right density (20 to 30 particles/m*l* or more) were mostly dinoflagellates and were generally located in stratified layers near the chlorophyll maximum (Table 1). Twenty to thirty particles per milliliter seemed to be a threshold quantity needed for successful first feeding. During this experiment at sea, a short (one day) storm arose which chased us into harbor. When I went back the next day, the stratified layers of larval food organisms were gone (Fig. 11). It was clear from this that wind-induced turbulence had diluted and disrupted the aggregation of food particles to below the threshold number needed by the anchovy first-feeding larva and this led me to hypothesize that turbulence might be correlated with larval anchovy survival and subsequent recruitment. In other words, stable ocean conditions favor the aggregation of suitably-sized food organisms so that above-threshold numbers of food particles become available to larvae.

Table 1. Results of a field experiment on the feeding of first-feeding anchovy larvae in relation to different concentrations of natural food, Numbers in ( ) refer to counts of the dinoflagellate *Gymnodinium splendens* at each depth. (after Lasker, 1975).

| No. | Date and Time A. Surf. Temp. B. Chl. Max., Temp. and Depth | Position | Total number particles/*ml* | | Feeding by Anchovy Larvae Percent of Larvae with: | |
|---|---|---|---|---|---|---|
| | | | 23–37 um Diameter | >37–299 um Diameter | 1/4 to full gut | 1–8 particles in gut |
| 1. | 3/20/74, 1250 | Malibu | | | | |
| | A. 15°C | | 14.2 | 4.1 (<1) | 2 | 15 |
| | B. 14.2°C. 12m. | | 37.3 | 38.0 (12) | 23 | 46 |
| 2. | 3/20/74, 1745 | Manhattan Beach | | | | |
| | A. 15.2°C. | | 23.1 | 6.1 (6) | 0 | 11 |
| | B. 14.5°C., 13.5m. | | 29.8 | 19.7 (12) | 0 | 18 |
| 3. | 3/21/74, 0900 | Seal Beach | | | | |
| | A. 15.8°C. | | 217.9 | 33.2 (<1) | 0 | 12 |
| | B. 14.2°C., 16.5m. | | 53.8 | 352.0 (380) | 22 | 24 |
| 4. | 321/74, 1340 | Laguna Beach | | | | |
| | A. — | | 34.0 | 9.0 (0) | 0 | 10 |
| | B. —, 15m. (no chl. max.) | | 29.0 | 5.7 (0) | 0 | 11 |
| 5. | 3/21/74, 1715 | Dana Point | | | | |
| | A. 15.5°C. | | 18.7 | 5.9 (<1) | 5 | 16 |
| | B. —, 15m. | | 55.2 | 23.2 (5) | 0 | 69 |
| 6. | 3/21/74, 1900 | San Onofre | | | | |
| | A. 15.2°C. | | 9.3 | 4.0 (<1) | 0 | 8 |
| | B. —, 19.5m. | | 42.4 | 47.7 (34) | 9 | 25 |
| 7. | 4/8/74, 1500 | San Onofre | | | | |
| | A. 17.1°C. | | 5.7 | 9.1 (<1) | 0 | 13 |
| | B. 14.8°C., 16m. | | 14.0 | 81.3 (64) | 9 | 40 |
| 8. | 4/10/74, 1710 | San Onofre | | | | |
| | A. 14°C. | | 8.4 | 14.1 (0) | 0 | 12 |
| | B. 13.5°C., 14m. (no chl. max.) | | 10.5 | 23.2 (0) | 0 | 15 |
| 9. | 4/11/74, 0915 | San Onofre | | | | |
| | A. 13.0°C., 5m. (no chl. max.) | | 6.4 | 10.5 (0) | 0 | 4 |

The following year (1975) a full scale oceanographic survey was mounted to test the effect of wind on stratification of larval anchovy-sized food particles (Lasker, 1978). Nature once again performed an interesting experiment. Although the weather was calm and the ocean stable and stratified, a red tide composed of the thecate dinoflagellate *Gonyaulax polyedra* dominated the anchovy larva's environment for first half the spawning season. Earlier we had found that *Gonyaulax* in the laboratory was eaten avidly by first feeding anchovy larvae but that the larvae would not grow and soon died (Scura and Jerde, 1977). In the midst of the spawning season, there was an onset of Northwesterly winds which normally cause upwelling off the coast of California. These winds were strong enough to induce massive upwelling which swept out *Gonyaulax* and brought in nutrient rich water resulting in a diatom bloom (Fig. 12). Our laboratory findings, however, showed that anchovy larvae do not eat diatoms. Thus, two poor phytoplankton food types were dominant in the larva's environment in 1975. The 1975 anchovy year class was the worst that had been recorded over a sixteen year recording period despite indicators to the contrary, such as an enormous spawning (Fig. 13), and great primary productivity (Fig. 14). My belief is that most of the larvae

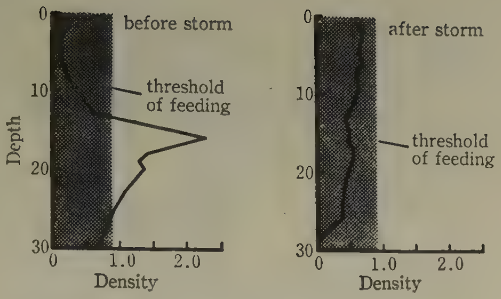

Fig. 11. The effect of a storm on the vertical distribution of larval food particles. The threshold for larval feeding was 30 particles per milliliter. The dark line indicates relative concentrations of food (dinoflagellates) with depth (after Lasker, 1975).

starved and were lost to the year class because the major food sources in their environment were unsuitable for growth and survival.

In 1978 I had another opportunity to study the habitat of the anchovy during its entire spawning season (Lasker, 1981). Early in the spawning season, December, 1977, a great storm occurred off the Pacific coast of the U.S. and was succeeded by frequent but less intense storms through March (Fig. 15). Precipitation in Southern California in the 1977–78 season set a 20 year record of 56 cm (100 year average = 25 cm). Furthermore, these storms covered a large geographic area,

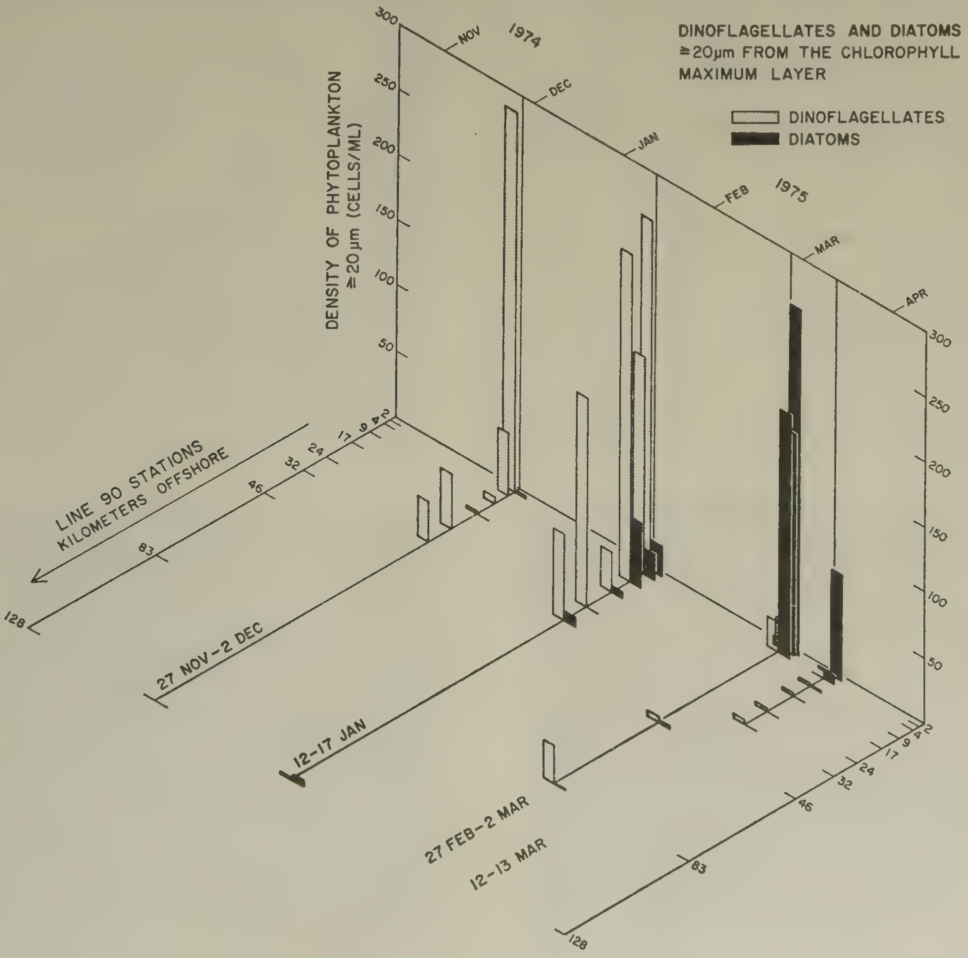

Fig. 12. Diatoms replace dinoflagellates as a result of an upwelling event in 1975 off California (from Lasker, 1978).

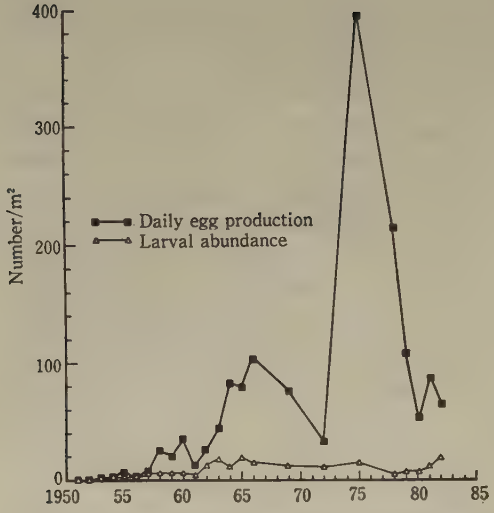

Fig. 13. Anchovy egg production off California from 1950 through 1982 (after Lo, 1984).

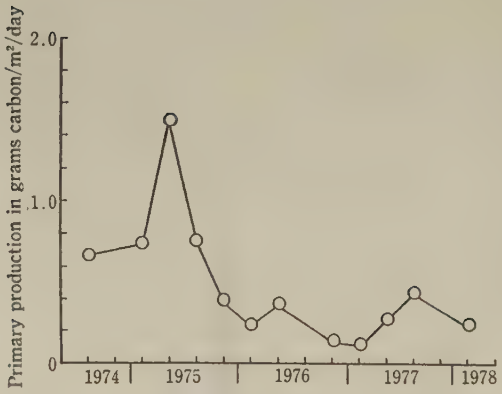

Fig. 14. Primary production in the Southern California Bight, 1974 through 1978 (modified from Smith and Eppley, 1982).

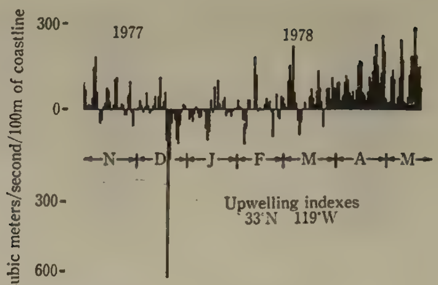

Fig. 15. Upwelling indexes 1977–1978, at San Clemente Island in the Southern California Bight (after Lasker, 1981). The values above the line indicate offshore flow; below the line, onshore flow.

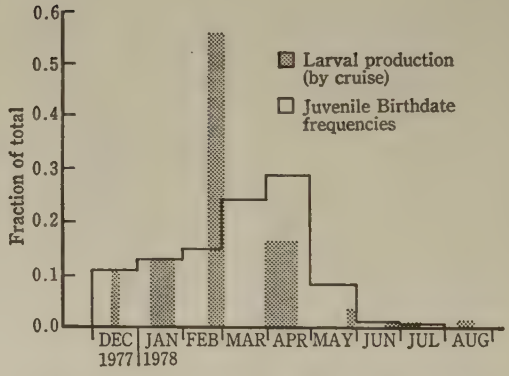

Fig. 16. Larval anchovy production compared to fractional survival of juveniles for the 1977–78 spawning season off California (after Methot, 1983).

affecting virtually all of the anchovy spawning habitat.

Based on my earlier work I expected to find no aggregations of organisms suitable for first-feeding anchovies and did not find any, although anchovy spawning continued unabated through the stormy periods. In March the storms ceased, stable conditions were re-established and prevailed to the end of the spawning season, early May. Stratification of anchovy larval food organisms was evident in mid–March and continued to the end of the spawning season.

I predicted that the 1978 year class would have very few survivors from the first half of the spawning season but that survival from mid–March to the end of spawning would be good to excellent. This prediction was confirmed by Methot (1983) who was able to show that the juvenile survivors of the 1978 year class had birthdate distributions which agreed with the prediction. A much larger number of survivors had been born from March to May than from December to March despite the fact that larval production was about equal in both halves of the spawning season (Fig. 16).

## § 9. Larval starvation

Because starvation in the sea may be an extremely important phenomenon, scientists at the Southwest Fisheries Center have tried to quantify starvation by using morphometric and histological methods. O'Connell (1976, 1980) developed histological criteria to determine if a larva was starving. An examination of his data by Theilacker (1986) showed that appreciable numbers of anchovy larvae can be found starving each day when tested histologically. For example, in March 1977, 35 to 46% of anchovy larvae were shown to be dying from starvation each day. Theilacker has also shown with jack mackerel larvae, *Trachurus symmetricus*, that at first-feeding they are mostly starving in oligotrophic (offshore) parts of their spawning environment but are mostly well fed in eutrophic areas, e.g. close to islands (Fig. 17).

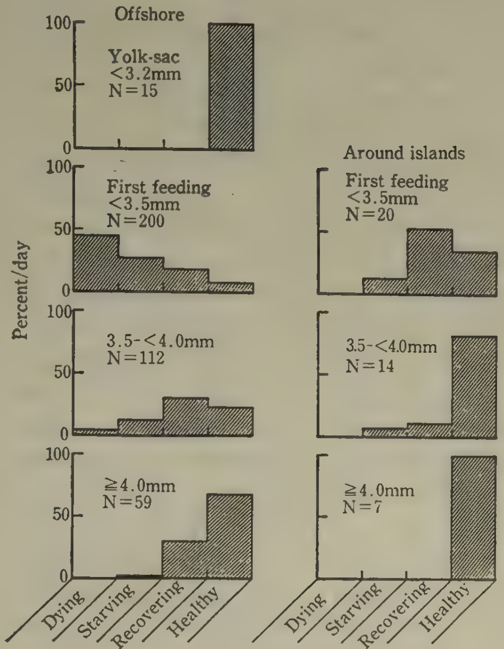

Fig. 17. Percent starvation in jack mackerel (*Trachurus symmetricus*) larvae in an offshore and an island environment (from Theilacker, 1986).

## § 10. Larval transport

Gyres, island wakes, fronts and upwelling plumes are the most prominent features of the California and Baja California coastal regime when viewed by infrared satellite (Lasker *et al.*, 1981) and by the Coastal Zone Color Scanner (Fiedler, 1983). The extent of water moving actively offshore was not really appreciated until satellite photos showed that there are "jets" of water streaming from the coast a hundred or more kilometers offshore in Eastern Boundary upwelling regions (Fig. 18). In

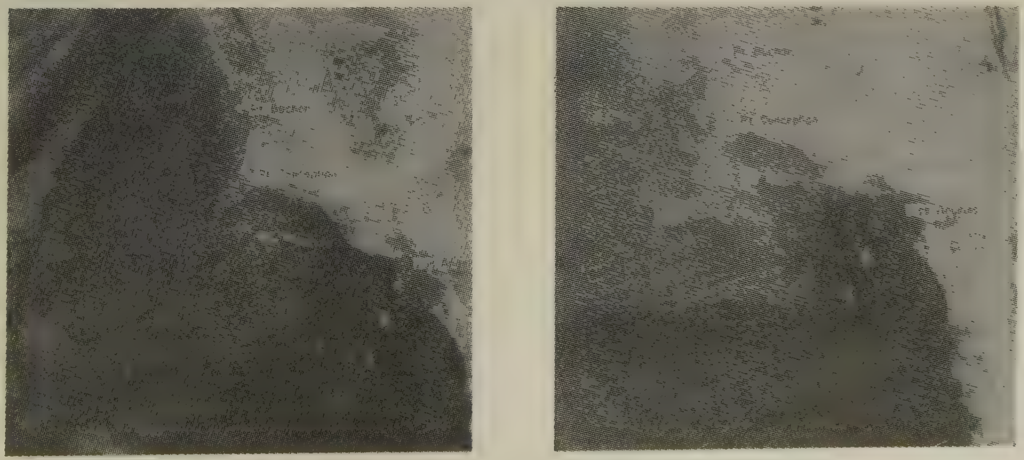

Fig. 18. Development of upwelling off the California Coast (left March 19, 1980; right: March 28, 1980 as) seen by an infrared satellite (after Lasker *et al.*, 1981).

recent studies at the SWFC we have shown that anchovy eggs and larvae, while usually confined to the Southern California Bight, occasionally are drawn far offshore into an extremely unfavorable habitat for larval survival. This kind of transport has been found to be associated with large gyres which induce water to flow strongly offshore (Fiedler, 1986).

Parrish *et al*. (1981) hypothesized that deviations from "normal" transport conditions could have profound detrimental effects on a year class by carrying eggs and larvae to areas where there is not enough food for the larvae to survive. Methot (1983) compared the 1978 and 1979 anchovy year classes and found that despite the relatively low survival in the first half of the spawning season, 1978 had one of the largest anchovy recruitments in years. Conversely, the 1979 year class had a very poor recruitment and he believed this difference could be explained by increased upwelling and larval transport of larvae into poor feeding areas offshore in 1979. In any event lack of food for larvae is still the basic hypothesis for poor year classes if offshore transport is invoked as a mechanism.

Although offshore transport is a possible mechanism that can be detrimental to the survival of a particular year class, over evolutionary time anchovies and sardines appear to have chosen the least energetic area (the Southern California Bight) and time (late Winter, early Spring) for spawning with respect to upwelling and offshore transport (Parrish *et al*. 1981). A comparison of wind mixing and stability indices for the major spawning regions of the three subpopulations of *Engraulis mordax* show that "peak spawning occurs during seasons and locations associated with stable stratification, relatively low rates of turbulent energy production, and weak offshore transport (upwelling)" (Husby and Nelson, 1982).

A comparison of the California and Peru Current anchovy stocks by Bakun and Parrish (1982) showed that there is "a consistent pattern of avoidance of centers of maximum upwelling, which are characterized by intense turbulent mixing and offshore transport. Large stocks tend to occur in regions of low turbulent mixing, downstream of upwelling maxima."

## § 11. Oceanographic explanations of differential recruitment

Several effects on larval anchovy survival by specific oceanographic events seem clear from the work we have done in California. First, upwelling can be either favorable or detrimental, depending on its timing and the biological response of anchovy larvae. For example, upwelling due to sustained northwest winds brings nutrients to the surface near shore and provides an excellent habitat for organisms that can be eaten by anchovy larvae, e.g. copepods. On the other hand, sustained and excessively strong upwelling, particularly during the anchovy's spawning season, can destroy the stratification needed to provide high enough concentrations of food for larval survival. Furthermore, it is also possible that with sustained upwelling larvae may be swept out to sea into unfavorable feeding environments. When the response to upwelling is the production of diatoms, anchovy larvae do not benefit directly and this may be particularly bad for first-feeding larvae, although older larvae benefit from the nauplii produced by copepods which are stimulated to reproduce by eating diatoms.

Storms can have enormous effects on larval survival by disrupting stratified larval food layers and by preventing restratification. My colleagues in La Jolla, Dr. Peterman and Mr. Bradford (1987) have analyzed 13 years of wind data where they correlated the average instantaneous mortality rate of northern anchovy larvae against the number of four day calm periods found in each month of the anchovy spawning season (Fig. 19). A highly significant correlation ($r=0.81$) was found further supporting the idea that stability is a necessary prerequisite to larval survival in this species.

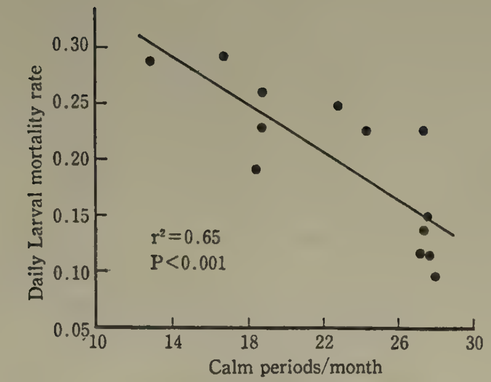

Fig. 19. Correlation between calm periods per month with daily anchovy (*Engraulis mordax*) larva mortality rate for a thirteen year data set (after Peterman and Bradford, 1987).

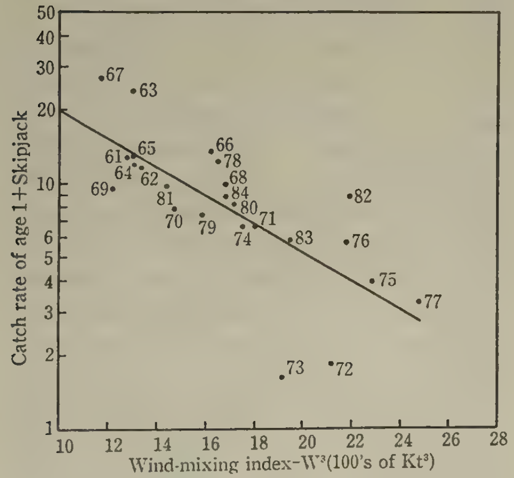

Fig. 20. Catch rate of age 1+ skipjack, *Kvtsuuonus pelamis* in thousands of fish per day in the equatoria Pacific Ocean correlated with wind speed cubed (after Forsbergh, 1986).

By analyzing 24 years of catch data, Forsbergh (In Press) has shown that there is a very good correlation between cube of the wind speed and the catch of one year old skipjack tuna over a large area of the Pacific Ocean (Fig. 20). Thus, the idea that stability is needed for the production of good year classes seems applicable to other fishes.

## §12. Older larvae and mortality curves

Hjort ignored older larvae in his hypothesis but many scientists believe that larval mortality over the entire larval period is more likely to determine recruitment than the heavy mortality seen in first-feeding larvae. This seems to be borne out by our inability to match up first-feeding larvae mortality rates with recruitment. The answer to the question of the involvement of any stage larva in determining recruitment is tied to our inability to determine the precise shape of the annual mortality curve. For anchovy our best mortality curves (Fig. 21) are derived from the number of eggs and larvae obtained over a 40 day period in the midst of the anchovy spawning season and from an area over thousands of square kilometers. Corrections are made for extrusions of eggs and larvae through the meshes of the plankton net, avoidance of the net as the larvae grow older, adjustment for individual growth rates and the application of two models, an age-independent instaneous mortality rate for eggs and an age-dependent mortality rate (a) for larvae (Lo, 1986). The imprecision of these curves makes it difficult to interpret whether some particular time in the life cycle is a determinant of recruitment or not. Peterman *etal.*(1986), using sophisticated statistical techniques has shown first-feeding larval anchovy

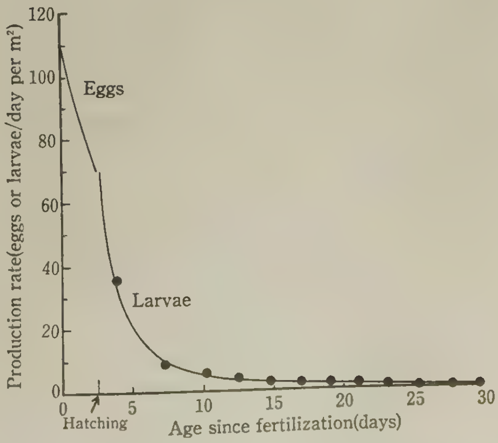

Fig. 21. Mortality curve of anchovy eggs and larvae (after Picquelle and Hewitt, 1983).

mortality and abundance are poor predictors of recruitment. Their data show that the entire larval period may have to be taken into account before significant correlations can be found with recruitment.

### §13. Predation

In our attempt to assign causes to egg and larval mortality, the work in La Jolla has also centered around another hypothesis, that predation is the major cause of larval mortality. Since the paper by Lillelund and Lasker (1971) which implicated various copepods as possible consumers of first-feeding fish larvae, there have been a large number of studies on marine organisms consuming fish larvae, such as euphausiid shrimps (Theilacker and Lasker, 1974), ctenophores and coelenterates (Purcell, 1985; Bailey and Batty, 1984), chaetognaths (Alvariño, 1985) and fishes (Hunter and Kimbrell, 1980). New work at the Southwest Fisheries Center by Theilacker and her associates (1986) has demonstrated the use of an immunoassay to detect euphausiid predation on yolk-sac anchovy larvae. However, the conclusion one must come to at present is that, like every organism in the sea, there is the possibility that an anchovy larva will be eaten, but thus far with an unknown probability.

### §14. Density dependent regulation of populations

It is particularly difficult to assign density effects to the fluctuation of clupeoid populations. From the example of the Japanese sardine, there seems to be no minimum stock size which cannot give rise to a reasonable year class given that the conditions are right. There is, on the other hand, reasonable evidence to indicate that in some instances two species may interact in some way so that it appears as if one affects the other. In California, the rise of the anchovy population during the decline of the sardine (Fig. 22) suggests this possibility while in Peru and Chile the sardine population increased greatly when the anchovetta collapsed (Fig. 5). Mr. Butler of my laboratory has correlated sardine larval mortality coefficients against anchovy biomass and concludes that cannibalism by anchovies on sardine eggs and larvae was a highly probable cause of the sardine's demise off California (Butler, 1987).

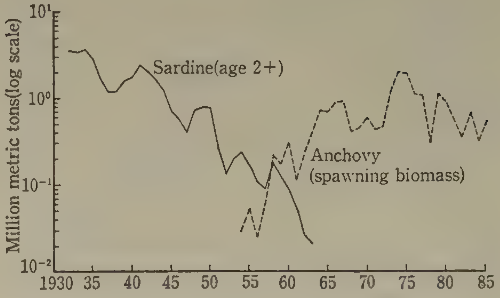

Fig. 22. Sardine and anchovy biomasses off the West Coast of the United States.

In La Jolla, one of the important needs for managing the anchovy fishery was an accurate method for determining biomass. We devised an egg production method technique for doing so (Lasker, 1985) and now have 6 years of data on the egg

Table 2. Anchovy egg production, spawning biomass and other adult parameters measured with the egg production method of biomass assessment, 1980 through 1985; coefficients of variation are not shown (see Fiedler *et al.*, 1986).

| YEAR | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 |
|---|---|---|---|---|---|---|
| Spawning female weight, g | 17.50 | 13.37 | 18.83 | 11.20 | 12.02 | 14.49 |
| Female fraction | .475 | .501 | .472 | .549 | .582 | .609 |
| Batch fecundity for average female | 7788 | 8208 | 10845 | 5297 | 5485 | 7343 |
| Spawning incidence, per day | .145 | .106 | .120 | .094 | .160 | .120 |
| Specific fecundity, eggs/day-g | 30.28 | 33.03 | 32.53 | 24.35 | 42.43 | 37.00 |
| Egg production, $10^{12}$ eggs/day | 26.34 | 20.96 | 13.51 | 17.25 | 12.98 | 16.95 |

Table 3. Effects of the 1983 El Niño on adult anchovies (from Fiedler *et al.*, 1986).

| Year | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 |
|---|---|---|---|---|---|---|
| Spawning biomass, in $10^3$ metric tons | 870 | 635 | 415 | 652 | 306 | 458 |
| Spawning female weight, g | 17.5 | 13.4 | 18.8 | 11.2 | 12.0 | 14.5 |
| Mean age in February, yrs | 1.80 | 1.80 | 2.46 | 1.29 | 1.76 | 1.46 |
| Year class size, $10^9$ fish | 63 | 14 | 45 | 35 | 109 | 39 |

production and interannual fluctuation in spawning biomass. These data are given in Table 2. They show that the spawning biomass of anchovies has been increasing off California and that there is a reasonable consistency in the biological parameters of the anchovy (such as egg production, fecundity and frequency of spawning) but with changes brought on by an El Niño event which occurred in 1982–1983.

### §15. El Niño

One of the most impressive environmental events affecting clupeoid populations is the massive warming of the eastern Pacific, known as El Niño. The El Niño conditions of 1982–1983 were the most impressive of the century and affected fisheries from Peru to California (Table 3). Both in California and Peru there is evidence that zooplankton production was far below normal. In Peru this resulted in great losses in body weight per fish (30% for anchovies; 15% sardines) and much lower egg production (Arntz, 1986). Our California data shows a similar loss in female weight in 1983, a lowered frequency of spawning and a low batch fecundity, but despite this, the number of eggs produced by the population was about average because the anchovy population was somewhat larger in 1983 than it was in 1982 and there were many first year spawners (a result of the warmer water) in contrast to previous years (Fiedler, *et al.* 1986). As far as this large El Niño event is concerned, the effect on fisheries, even in Peru, seems to be due to changes in the distribution of fishes and their availability rather than to changes in the size of the population or the number of eggs spawned.

### §16. The sardine/anchovy recruitment project

The work I discussed earlier provides the basis for a study of recruitment that we have never been able to do before. We are now able to analyze events within a spawning season and to determine the effect of specific oceanographic events on monthly survival and mortality of larvae. In conjunction with cohort analyses we may be able to tell what determined the strength of a particular year class.

The Intergovernmental Oceanographic Commission (I.O.C.) and the Food and Agriculture Organization of the United Nations have endorsed a program encompassing this idea called SARP or the Sardine/Anchovy Recruitment Project. I wish to outline how such a program would be put together, what measurements need to be taken, what area needs to be sampled and what can be expected to be deduced from the data collected.

### §17. Larval production

The basis for SARP is the comparison between the measured larval production by month and the survivorship by month as deduced from the birthdates of large larvae and juveniles (Methot, 1983). The development of the accurate ageing of fish larvae and juveniles by counting daily rings on the otoliths has provided the fishery biologist with a powerful tool for studying recruitment. We have calibrated the rings by counting the increments on otoliths taken from larvae of known age (Brothers *et al.*, 1976) and have proven them to be daily. Since then many fish species have been examined and have been seen to have daily increments.

Because the anchovy has a protracted spawning season from January through May, it is now possible to correlate environmental events occurring within the season with larval survival. If follows that most of the clupeoids can be studied in this way. For a complete analysis, additional information is important such as the number and strength of cohorts, the number of eggs spawned, the spawning biomass, the number and distribution of predators, larval production, the proportion of starving larvae, larval growth rates, mortality rates of all egg and larval stages, and an assessment of older larvae throughout the spawning season. The egg production method of anchovy biomass assessment that I mentioned earlier provides many of these parameters, while the fishery statistics gives the recruit and adult fish information.

Thus a minimum plan for recruitment studies was decided on by an I.O.C. working group.

1) A quantitative larval survey and an egg production method biomass survey must be done.
2) Large larvae and juveniles must be sampled sufficiently to determine birthdates by the otolith daily ring method.
3) Physical oceanographic measurements and monitoring must be done over the spawning season.
4) Meteorological measurements (especially winds) should be taken from ship and shore.
5) A quantitative analysis of year class strength must be done from fisheries statistics.

Sardines and anchovies are prime candidates for these studies because they meet all the criteria for success, such as a protracted spawning season, easy to read otoliths, multiple spawning behavior, discreet stocks, and a highly variable population. Furthermore these are fishes of commercial importance with adequate sampling and statistics collection already in place, and with a known geographical distibution.

## References

Alvariño, A.(1985): Predation in the plankton realm; mainly with reference to fish larvae. *Investigaciones Marinas CICIMAR*, 2, 1–122.

Arntz, W. E. (1986): The two faces of El Niño 1982–83. *Meeresforsch.*, **31**, 1–46.

Bailey, K. M. and R. S. Batty (1984): Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. *Marine Biology*, **83**, 287–291.

Bakun, A. and R. H. Parrish (1982): Turbulence, transport, and pelagic fish in the California and Peru Current systems. *Calif. Coop. Oceanic Fish. Invest. Rep.*, **23**, 99–112.

Barber, R. T., W. W. Kirby Smith and P. E. Parsley (1980): Wetland alteration for agriculture, p. 642–651. *In* P. E. Greeson, J. R. Clark and J. E. Clark (eds.), Wetland Functions and Values, Amer. Wat. Res. Assoc., Minneapolis, MN.

Brothers, E. B., C. P. Mathews and R. Lasker (1976): Daily growth increments in otoliths from larva and adult fishes. *Fish. Bull. U. S.*, **74**, 1–8.

Butler, J. (1987): Comparison of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph. D. Thesis, U. C. S. D., San Diego, 242pp.

Clark, F. N. and J. C. Marr (1955): Population dynamics of the Pacific sardine. *Calif. Coop. Oceanic Fish. Invest. Rep.*, **4**, 11–48.

Fabre-Domergue and E. Biétrix (1905): Développement de la Sole (*Solea vulgaris*). Introduction à l'étude de la pisciculture marine. Travail du Laboratoire de Zoologie Maritime de Concarneau. Vuibert et Nony, Paris. 243pp.

Fiedler, P. C. (1983): Satellite remote sensing of the habitat of spawning anchovy in the Southern California Bight. *Calif. Coop. Oceanic Fish. Invest. Rep.*, **24**, 202–209.

Fiedler, P. C. (1986): Offshore entrainment of anchovy spawning habitat, eggs, and larvae by a displaced eddy in 1985. *ibid.*, **27**. 144–152.

Fiedler, P. C., R. D. Methot and R. P. Hewitt (1986): Effects of California El Niño 1982–84 on the northern anchovy. *J. Mar. Res.*, **44**, 317–338.

Forsbergh, E. D. (1986): The influence of environmental variables on the apparent abundance of skipjack tuna (*Katsuwonus pelamis*) in the fisheries of the eastern Pacific Ocean. *Bull. Inter. Amer. Trop. Tuna Comm.* (in Press).

Hjort, J. (1914): Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P. -V. des Réun. Cons. Perm. int. Explor. Mer*, **20**, 1–228.

Hjort, J. (1926): Fluctuations in the year class of important food fishes. *Jour. du Conseil*, **1**, 5–39.

Hunter, J. R. and S. R. Goldberg (1980): Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fish. Bull. U. S.*, **77**, 641–652.

Hunter, J. R. and C. A. Kimbrell (1980): Egg cannibalism in the northern anchovy, *Engraulis mordax. Fish. Bull. U. S.*, **78**, 811–816.

Husby, D. M. and C. S. Nelson (1982): Turbulence and vertical stability in the California Current. *Calif. Coop. Oceanic Fish. Invest.*, **23**, 113–129.

Kondo, K. 1980: The recovery of the Japanese sardine–the biological basis of stock-size fluctuations. *Rapp. P.-V. Réun. Cons. int Explor. Mer*, **177**, 332–354.

Kramer, D. and E.H. Ahlstrom (1968): Distributional atlas of fish larvae in the California Current region: Northern anchovy, *Engraulis mordax* Girard, 1951 through 1965. *Calif. Coop. Oceanic Fish. Invest. Atlas*, **9**, 269 pp.

Lasker, R. (1975): Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. U. S.*, **73**, 453–462.

Lasker, R. (1978): The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-V. Réun. Cons. int. Explor. Mer*, **173**, 212–230.

Lasker, R. (1981): Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting years, 1975 through 1978. *ibid.*, **178**, 375–388.

Lasker, R.(ed). 1985: An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax. Nat. Oceanic Atmos. Admin. Tech. Rep. NMFS*, **36**, 99pp.

Lasker, R., J. Pelaez and R. M. Laurs (1981): The use of satelite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). *Remote Sensing of Environment*, **11**, 439–453.

Laurs, R. M., P. C. Fiedler and D. R. Montgomery (1984): Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Research*, **31**, 1085–1099.

Laurs, R. M. and R. J. Lynn (1977): Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with transition zone waters. *Fish. Bull. U. S.*, **75**, 795–822.

Lillelund, K. and R. Lasker (1971): Laboratory studies of predation by marine copepods on fish larvae. *ibid.*, **69**, 655–667.

Lo, N.C.H. (1986): Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. *ibid.*, **84**, 395–407.

Marr, J. C. (1960): The causes of major variations in the catch of the Pacific sardine *Sardinops caerulea* (Girard). *Proc. World Scientific Meeting on the Biology of sardines and related species*, **3**, 667–791.

Methot, R. D. Jr., (1983): Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. *Fish. Bull., U. S.*, **81**, 741–750.

Murphy, G. T. (Chairman) (1974): Report of the fourth session of the panel of experts on stock assessment on Peruvian anchoveta. *Instituto del Mar del Perú (Callao), Bol.* **2**, 605–719.

O'Connell, C. P. (1976): Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. *J. Exp. Mar. Biol. Ecol.*, **25**, 285–312.

O'Connell, C. P. (1980): Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. *Fish. Bull.*, **78**, 475–489.

O'Connell, C. P. and L. P. Raymond (1970): The effect of food density on survival and growth of early post yolk sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. *J. Exp. Mar. Biol. Ecol.*, **5**, 187–197.

Parrish, R. H., C. S. Nelson and A. Bakun (1981): Transport mechanisms and reproductive success of fishes in the California Current *Biol. Oceanogr.*, **1**, 175–203.

Peterman, R. M. and M. J. Bradford (1987): Wind speed index correlates with mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science*, **235**, 354–356.

Peterman, R. M., M. J. Bradford, N. C. H. Lo and R. D. Methot (In Press): Contribution of early life stages to interannual variability in recruitment of northern anchovy, *Engraulis mordax. Can. J. Fish. Aquat. Sci.*

Picquelle, S. J. and R. P. Hewitt (1983): The northern anchovy spawning biomass for the 1982–83 California fishing season. *Calif. Coop. Oceanic Fish. Invest. Rep.*, **24**, 16–28.

Purcell, J. E. (1985): Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull. Mar. Sci.*, **37**, 739–755.

Schumacher, A. (1980): Review of North Atlantic catch statistics. *Rapp. P. -V. Réun. Cons. Int. Explor. Mer*, **177**, 8–22.

Scura, E. D. and C. W. Jerde (1977): Various species of phytoplankton as food for larval northern anchovy, *Engraulis mordax* and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. *Fish. Bull. U. S.*, **75**, 577–583.

Sette, O. E. (1943): Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). Structure of a research program to determine how fishing affects the resource. *U. S. Dept. Interior, Spec. Sci. Rep.*, **19**, 27pp.

Smith, P. E. and R. W. Eppley (1982): Primary production and the anchovy population in the Southern California Bight: Comparison of time series. *Limnol. Oceanogr.*, **27**, 1–17.

Soutar, A. and J. D. Isaacs (1974): Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fish. Bull. U. S.*, **72**, 257–273.

Tanaka, S. (1983): Variation of pelagic fish stocks in waters around Japan. *In* G. D. Sharp and J. Csirke (eds.), Proc. of the Expert Consultation to Examine Changes in Abundance in Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, **291**, Vol. 2, 17–36, Rome.

Theilacker, G. H. (1986): Starvation induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. *Fish. Bull. U. S.*, **84**, 1–17.

Theilacker, G. H. and R. Lasker (1974): Laboratory studies of predation by euphausiid shrimps on fish larvae. The Early Life History of Fish, J. H. S. Blaxter, ed., Springer Verlag, Berlin, p. 287–299.

Theilacker, G. H., A. S. Kimball and J. S. Trimmer (1986): Use of an ELISPOT immunoassay to detect euphausiid predation on larval anchovy. *Marine Ecology-Progress Series*, **30**, 127–131.

Tsukayama, I. (1982): Recursos pelagicos y sus pesquerias en Peru. Seminario Regional sobre Recursos Pelagicos y sus Pesquerias en el Pacifico Sudeste, Guayaquil, Ecuador, 25–26 Oct. 1982.

# I-4. R. Lasker 博士の「カリフォルニア沖カタクチイワシの研究—その生物学・資源加入と水産海洋学—」について

川口弘一*

1949年に始まるカリフォルニア沖マイワシ資源の急減とそれに伴う漁業と缶詰業界の不況は，カリフォルニア州内とその周辺地域に大きな経済停滞をもたらした．これが契機となって魚の資源量変動研究のための国立研究所が設立され，それが現在の南西水産研究所（ラホヤ）の基となった．そして1950年代始めにカリフォルニア沖イワシに何が起きたかを明らかにするために共同研究組織が作られ，この活動が現在の CalCOFI となって続いている．この共同研究は初期段階から，カリフォルニア沖を一つの生態系としてとらえ，単にイワシのみを対象とするのではなく，すべての重要種を関連づけて研究してきた．イワシが減少する一方で，カタクチイワシ資源が増加しつつあったので研究の焦点もマイワシからカタクチに移り現在に到っている．

### (1) 漁獲圧力のない時代の大きな資源変動

カタクチイワシの生息域であるサンタバーバラ海盆の無酸素状態の海底から得られるコア（Varves と呼ばれる）は，数千年間層序が乱されていないことが分かっており，層別に年代確定ができる．このコア中に含まれるカタクチイワシ類，マイワシ類，タラ類の鱗の数を層別に計数し，各種の各年別の相対資源量を出したところ，漁獲圧力のない1800年代にも資源量変動が存在したことが明らかになってきた．

### (2) カリフォルニア沖イワシの研究の始まり

カリフォルニアでは，産卵期が12月から４月にかけて４カ月つづき，その間同一雌が20〜30回産卵することが明らかとなった．この知見により資源加入量が産卵親魚の数や総産卵量に影響される密度依存タイプなのか，それとも環境要因に影響される密度独立タイプなのかを研究する方法が我々に与えられた．そして，Hjot が大西洋のニシンについて出した “critical period” hypothesis に基づいてラホヤでの研究が進められた．しかし，初期の段階での仔魚の死因には飢餓だけでなく被捕食も重要であることが分かっている．

### (3) 飼育実験と野外実験

飼育実験の結果で最も注目すべきことは，仔魚の生残を確保するためには，実際の海で観測するよりもはるかに高密度の餌料を与えねばならないということであった．例えば，コペポーダノープリウスでは1000個体/*l* 以上の密度が必要だが，カリフォルニア沖では200個体/*l* 程度しか存在しない．そこで問題は好適サイズの餌が最適な密度で何処に存在するか，その分布を規定する要因は何かということにしぼられた．飼育した仔魚を船に乗せ，現場で各水深から採水を行い，その試水で仔魚を飼育することも行われた．その結果 20〜30個体/m*l* 以上の密度を示した鞭毛藻類が餌として好適サイズで，好適密度に分布していることが分かった．この種は *Gymnodinium splendes* で，飼育実験でもよい餌料ということが確められている．

### (4) 時化（しけ）と湧昇

*G. splendes* はクロロフィル極大層に高密度に集中分布するが，シケによる海の成層の乱れにより容易に分散し，摂餌開始期の仔魚の生残に重要な必要最低餌量密度以下になってしまうことがわかった．この他湧昇によって起こる沖への流れ出しによって，餌密度の低い外洋へ運搬される仔魚の量も生き残りにとって重要な要因であることも分かってきた．これと並行して野外採集仔魚の飢餓状態を組織学的に判定する方法を開発し，35〜46％の仔魚が毎日死亡しているという観測例も得られている．

### (5) 今後の展望

これまでの研究結果によれば，摂餌開始期の仔魚の生き残りだけから加入量を説明することは難しい．仔魚期全体を通じての生存率が加入量を決定していると考えら

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# STATUS OF THE WIDOW ROCKFISH FISHERY

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# ABSTRACT

Cohort and catch-at-age analysis were used to estimate fishing mortality rates and population size for widow rockfish (Sebastes entomelas), using 1980-1987 catch-at-age data. Fishing mortality was moderately higher in 1987 than in 1986, due to an increase in the harvest. Projections of stock biomass for 1988 and 1989 indicated that stock levels should be lower than the estimated levels in 1986 and 1987. The results indicated that the 1980 and 1981 year classes are strong. However the cohort analysis indicated that these year classes are much stronger than all but the 1970 year class, while the catch-at-age analysis indicates the two year classes are close to average values. While results from cohort analysis indicates that the stock is close to 1980 levels, results from catch-at-age analysis indicates that the stock at the beginning of 1988 was 30-35 percent of the 1980 level, and at the beginning of 1989 will be about 30 percent of the 1980 level. Using results from cohort analysis, estimates of MSY ranged from 8,200 to 13,300 mt, with an average of 10,700 mt. The recommended fishing mortality rate for fully recruited fish was 0.30, if M = 0.20 and 0.25, if M = 0.15. At this level of fishing effort, average yield in 1989 and 1990 (an estimate of ABC) would be 17,200 mt. Using results of catch-at-age analysis, estimates of MSY ranged from 5,900 to 11,400 mt, with an average of 8,400 mt. At the recommended fishing mortality rates for fully recruited fish, average yield in 1989 and 1990 would be 7,600 mt. Because of the considerable uncertainty in the status of the stock we recommend that ABC be set at the average estimate of MSY (9,500 mt). The recommended ABC is 21 percent below the 1988 ABC and slightly higher than average landings between 1983 and 1986.

# INTRODUCTION

This report represents an update of the widow rockfish (Sebastes entomelas) status report submitted in August 1987 (Hightower and Lenarz 1987). Included is (1) a review of the 1987 report and of recent events in the fishery, (2) estimates of the current status of the stock, (3) and recommendations for harvest in 1989.

# SUMMARY OF PREVIOUS ASSESSMENT

The estimate of acceptable biological catch (ABC) for 1988 was 12,100 mt, a decrease of 400 mt from the 1987 ABC. The stock was estimated to above the maximum sustained yield (MSY) level because of the relatively large 1977-1980 year classes. Estimates of total stock biomass projected a decline from 1987 to 1988 and that spawning stock would remain the same or show a slight decline.

# RECENT HISTORY OF THE FISHERY

Landings in 1987 were higher than in 1986, due to increased landings in the northern part of the Columbia International North Pacific Fisheries Commission (INPFC) Area (Table 1, Figure 1). An increase in OY to 12,500 mt allowed the increased harvest. The fishery proceeded at a

Table 1. Landings (metric tons) of widow rockfish by area and year from 1979 through 1987.

| Year | INPFC Vancouver | N. Columbia | S. Columbia | INPFC Columbia | INPFC Eureka | INPFC Monterey-Con. | Total |
|---|---|---|---|---|---|---|---|
| 1979 | 329 | 432 | 1,894 | 2,326 | 2,166 | 120 | 4,941 |
| 1980 | 143 | 9,426 | 5,781 | 15,207 | 4,736 | 304 | 20,390 |
| 1981 | 1,991 | 7,969 | 12,301 | 20,270 | 3,430 | 2,000 | 27,691 |
| 1982 | 3,969 | 4,625 | 6,929 | 11,554 | 3,993 | 6,997 | 26,513 |
| 1983 | 1,596 | 2,490 | 2,129 | 4,619 | 2,442 | 1,554 | 10,211 |
| 1984 | 594 | 2,086 | 3,747 | 5,833 | 2,256 | 988 | 9,671 |
| 1985 | 446 | 2,128 | 2,993 | 5,120 | 2,313 | 977 | 8,856 |
| 1986 | 557 | 3,508 | 2,662 | 6,170 | 1,632 | 971 | 9,330 |
| 1987 | 496 | 6,603 | 2,689 | 9,292 | 1,598 | 799 | 12,185 |
| Total | 10,121 | 39,267 | 41,125 | 80,391 | 24,566 | 14,710 | 129,788 |

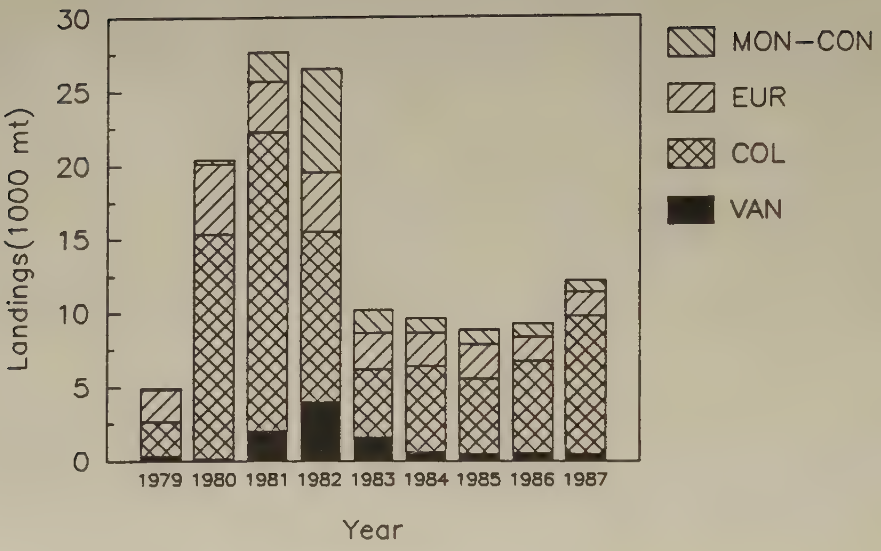

Figure 1. Landings of widow rockfish by INPFC area from 1979-1987.

faster rate in 1987 than in 1986, even though there continued to be good fishing for pink shrimp (Pandalus jordani). There were reports that schooled fish were more available in the Northern Columbia Area than in the past few years. We are not aware of changes in the availability of widow rockfish in other areas.

The 1980 and 1981 year classes dominated the catch numerically in 1987, although as in earlier years, the 1977-1979 year classes were also an important component (Table 2, Figure 2). Also as in earlier years, a large percentage of the 1987 catch (76 percent by number) was comprised of fish less than age 9, the age at 95 percent maturity (Figure 3). As of 1987, peak catches have occurred for all year classes through 1978.

The OY for 1988 was set at 12,100 mt which was the estimate of ABC (Hightower and Lenarz 1987). Vessels have been restricted to 30,000 lb trip limits with no more than one trip per week. Preliminary estimates are that 1988 landings will be about 12,100 mt, and that it will be necessary to place the fishery on more restrictive trip limits in October or November to avoid exceeding OY.

## ASSESSMENT METHODOLOGY

The approaches and assumptions used in the 1987 assessment were similar to those used in this assessment. Some changes were made in response to the SSC review of the 1987 assessment and reconsideration of the assumptions (See Appendix I for a review of the 1987 assessment by a member of the SSC.)

Population fecundity is used to estimate spawning potential instead of the biomass of mature fish. The population fecundity of an age group is the portion of mature females times the fecundity times the number of fish. The total population fecundity is the sum of age specific population fecundity over all age groups. We believe that population fecundity is likely to be more closely related to spawning potential of the stock than is biomass of mature fish. Population fecundity gives slightly more weight to older fish than biomass of mature fish. Relationship(s) between age and viability of released larvae are not known. Estimates of age specific average weight, portion of mature females and fecundity are shown in Table 3.

As before, all analyses were done using two levels for the instantaneous rate of natural mortality (M). These assumed rates were based on a catch curve analysis, and were thought to be approximate lower (0.15) and upper (0.20) bounds for M.

Since the 1985 assessment (Lenarz and Hightower, 1985), cohort analysis (Murphy, 1965) has been done by linking adjacent cohorts, under the assumption that F was equal for 9- and 10-year-old fish in a given year. For the 1970 through 1978 cohorts, we used the same starting value used in the 1985, 1986 and 1987 assessments ($F_9(1984)$). This starting value was originally selected (1985 assessment) by varying $F_9(1984)$ until we produced a decline in average F of about 50 percent from 1982 to 1983.

Table 2. Estimates of the number of widow rockfish landed by year class (millions) from 1980 through 1987.

| Year Class | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | Total |
|---|---|---|---|---|---|---|---|---|---|
| 65+ | 1.856 | 1.409 | 2.945 | 1.357 | 0.810 | 0.473 | 0.493 | 0.329 | 9.672 |
| 66 | 0.567 | 0.579 | 0.826 | 0.191 | 0.116 | 0.062 | 0.062 | 0.046 | 2.449 |
| 67 | 0.855 | 0.853 | 1.093 | 0.279 | 0.144 | 0.073 | 0.061 | 0.084 | 3.442 |
| 68 | 1.675 | 1.356 | 1.403 | 0.365 | 0.237 | 0.093 | 0.090 | 0.116 | 5.335 |
| 69 | 2.237 | 2.194 | 1.647 | 0.364 | 0.338 | 0.067 | 0.085 | 0.107 | 7.039 |
| 70 | 5.590 | 5.633 | 3.849 | 0.690 | 0.744 | 0.400 | 0.338 | 0.214 | 17.458 |
| 71 | 3.580 | 5.130 | 1.960 | 0.391 | 0.392 | 0.173 | 0.084 | 0.138 | 11.848 |
| 72 | 0.904 | 1.483 | 0.727 | 0.222 | 0.102 | 0.047 | 0.036 | 0.044 | 3.565 |
| 73 | 0.460 | 0.885 | 0.933 | 0.272 | 0.170 | 0.037 | 0.049 | 0.048 | 2.854 |
| 74 | 0.454 | 1.626 | 1.513 | 0.322 | 0.189 | 0.148 | 0.166 | 0.144 | 4.562 |
| 75 | 0.300 | 2.219 | 1.924 | 0.620 | 0.471 | 0.268 | 0.241 | 0.211 | 6.254 |
| 76 | 0.001 | 0.690 | 1.512 | 0.705 | 0.576 | 0.292 | 0.156 | 0.112 | 4.044 |
| 77 | 0.000 | 0.899 | 2.599 | 2.484 | 3.046 | 1.801 | 1.267 | 0.907 | 13.003 |
| 78 |  | 0.000 | 0.510 | 2.272 | 3.338 | 3.786 | 2.210 | 1.072 | 13.118 |
| 79 |  |  | 0.015 | 0.334 | 0.516 | 1.402 | 1.580 | 2.126 | 5.973 |
| 80 |  |  |  | 0.015 | 0.026 | 0.920 | 2.610 | 5.633 | 9.204 |
| 81 |  |  |  |  | 0.002 | 0.053 | 0.623 | 3.102 | 3.780 |
| 82 |  |  |  |  |  | 0.001 | 0.030 | 0.474 | 0.505 |
| 83 |  |  |  |  |  |  | 0.000 | 0.066 | 0.066 |
| 84 |  |  |  |  |  |  |  | 0.006 | 0.006 |

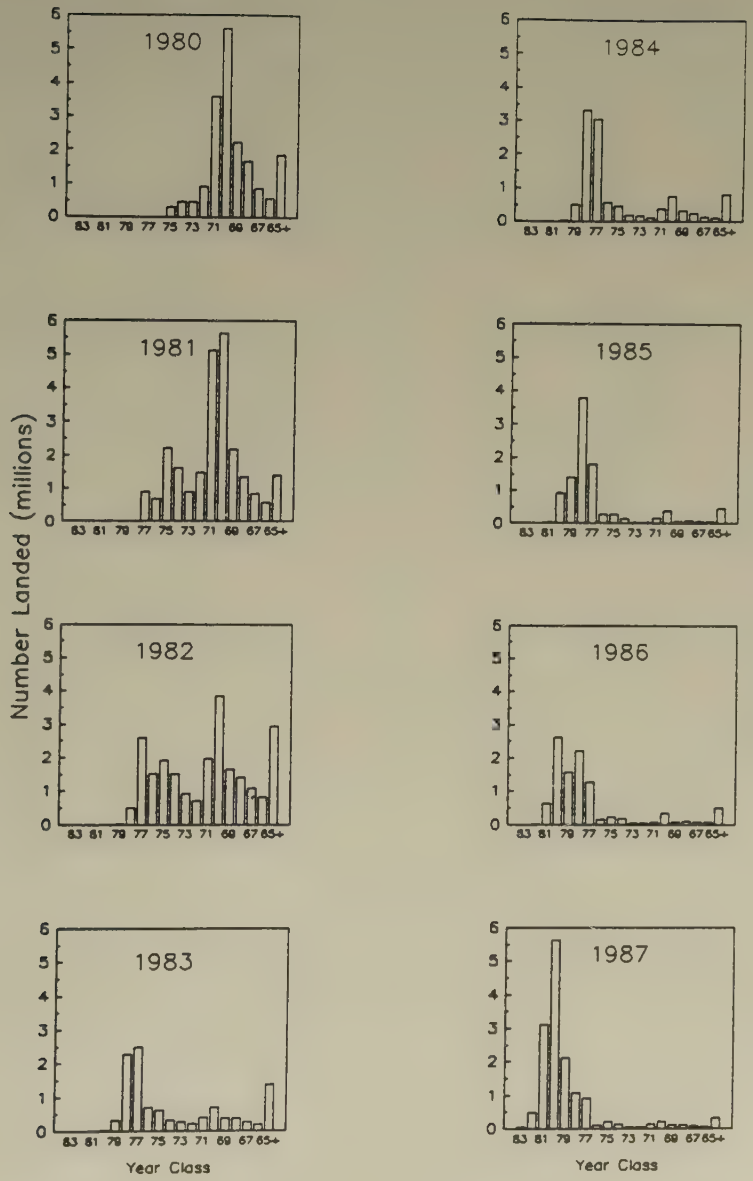

Figure 2. Total numbers of widow rockfish from each cohort in Washington, Oregon, and California landings from 1980-1987.

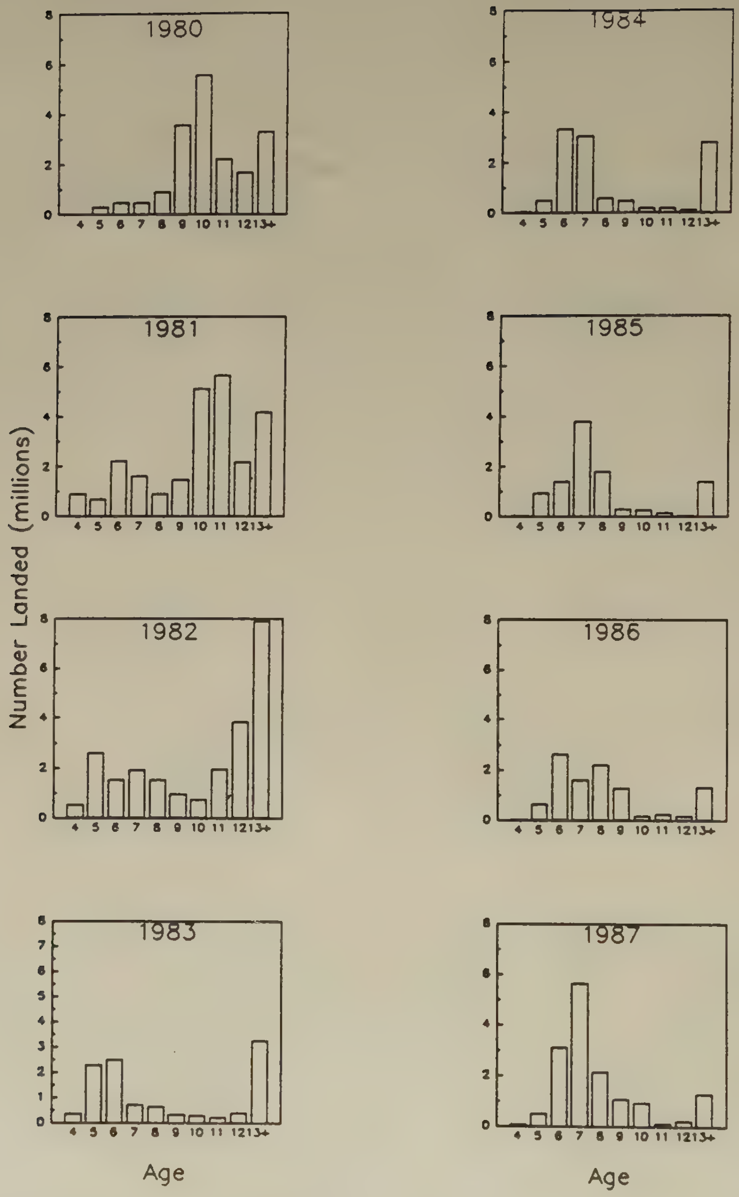

Figure 3. Total numbers of widow rockfish from each age group in Washington, Oregon, and California landings from 1980-1987.

Table 3. Estimates of weight, portion mature and fecundity by age.
Data sources:
Weight at Age: Barss and Wyllie Echeverria (1987) and Lenarz (1987)
Portion Mature at age (Oregon Females): Barss and Wyllie Echeverria (1987)
Fecundity at Age: Boehlert et al (1982)

| Age(years) | Weight (kg) | Portion Mature | Fecundity (Million Oocytes) |
|---|---|---|---|
| 5 | 0.5 | 0.15 | 0.006 |
| 6 | 0.6 | 0.17 | 0.017 |
| 7 | 0.7 | 0.70 | 0.114 |
| 8 | 0.9 | 0.79 | 0.224 |
| 9 | 1.0 | 0.95 | 0.327 |
| 10 | 1.1 | 0.97 | 0.392 |
| 11 | 1.2 | 0.97 | 0.451 |
| 12 | 1.3 | 1.00 | 0.526 |
| 13+ | 1.6 | 1.00 | 0.707 |

Regulations of the fishery should have resulted in significant drops in fishing mortality, and a 50 percent drop seems reasonable because the fishery essentially was closed in September 1983 and there were severe trip limits during the earlier part of the year. When $F_9(1984)$ was set to 0.3 to determine if higher values were reasonable, estimates of F for older fish became too high. Starting F values for cohorts younger than 1978 were obtained by assuming that the ratio of F for ages less than 9 to age 9 was the same in 1987 as in earlier years. For example, the estimate of $F_8(1987)$ was obtained by multiplying $F_9(1987)$ by(Ave. $F_8$)/(Ave. $F_9$), where (Ave. $F_8$) and (Ave.$F_9$) were averages for years 1980-1986. Starting F values for cohorts older than 1970 were obtained by using the same ratio method, except that estimates of mean F were obtained for the years 1981-1987. As in earlier assessments, the microcomputer program GENCOH was used for the cohort analysis.

Catch-at-age analysis was done using CAGEAN, a microcomputer program developed for use with Pacific halibut (Deriso et al. 1985). The approach differs from cohort analysis in several ways. The most important difference is that fishing mortality is assumed to be separable into a product of an age-specific selectivity coefficient $s_a$ and a full-recruitment fishing mortality rate F(k):

$$F_a(k) = s_a F(k)$$

where $F_a(k)$ is the fishing mortality rate for age-a fish in year k and $s_a = 1$ for at least one age. The separability assumption is important because it reduces the number of unknown fishing mortality parameters from 72 (8 years X 9 ages) to 16 (8 fishing mortality rates plus 8 selectivity estimates (with $s_{10}$ assumed to be 1)). Almost as important is that cohort analysis assumes that catches are known without error while catch-at-age analysis allows errors.

Several studies have noted that catch-at-age data are insufficient to estimate stock abundance reliably, because estimates of F and N have a large negative correlation (see Deriso et al. 1985). To stabilize parameter estimates, one of two types of auxiliary information can be used: additional information about model parameters or additional assumptions about stock dynamics (Deriso et al. 1985). For our catch-at-age analysis, we used the same assumptions about relative changes in F from year to year that were used to determine appropriate starting F's for cohort analysis. These assumptions were incorporated into the catch-at-age analysis by using average F's from cohort analysis as a relative measure of fishing effort (the annual averages shown in Table 4). In the previous assessment no weight was used to estimate average F. This year we decided that it would appropriate to weight F at age by catch at age in numbers, because the parameters of CAGEAN are estimated by minimizing deviations from observed catch at age. A model parameter (lambda) adjusts the amount of influence given to the "effort" data. If lambda=0, no relationship between F and effort is assumed. If lambda=1000, the relationship between F and effort is essentially exact (Deriso et al. 1985). Results from catch-at-age analyses of Pacific halibut data were similar for lambda values of 0.1 to 1.0 (Deriso et al. 1985), and production runs are done using the value 0.5 (P. R. Neal, unpublished documentation of CAGEAN program). Because we wished to

Table 4. Estimates of F for widow rockfish by age and year obtained by cohort analysis. Annual averages weighted by catch in number.

M = 0.15

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | Ave. |
|---|---|---|---|---|---|---|---|---|---|
| 5 | 0.030 | 0.102 | 0.096 | 0.082 | 0.018 | 0.013 | 0.012 | 0.024 | 0.047 |
| 6 | 0.073 | 0.297 | 0.318 | 0.119 | 0.159 | 0.058 | 0.042 | 0.073 | 0.142 |
| 7 | 0.108 | 0.379 | 0.428 | 0.227 | 0.197 | 0.257 | 0.081 | 0.115 | 0.224 |
| 8 | 0.201 | 0.295 | 0.686 | 0.224 | 0.277 | 0.162 | 0.222 | 0.141 | 0.276 |
| 9 | 0.227 | 0.551 | 0.542 | 0.281 | 0.250 | 0.208 | 0.156 | 0.151 | 0.296 |
| 10 | 0.227 | 0.551 | 0.542 | 0.281 | 0.250 | 0.208 | 0.156 | 0.151 | 0.296 |
| 11 | 0.217 | 0.355 | 0.396 | 0.296 | 0.268 | 0.298 | 0.277 | 0.152 | 0.282 |
| 12 | 0.226 | 0.323 | 0.412 | 0.120 | 0.203 | 0.082 | 0.602 | 0.393 | 0.295 |
| 13+ | 0.226 | 0.323 | 0.412 | 0.120 | 0.203 | 0.082 | 0.602 | 0.393 | 0.295 |
| Ave | 0.214 | 0.387 | 0.397 | 0.138 | 0.187 | 0.163 | 0.188 | 0.140 | |

M = 0.20

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | Ave |
|---|---|---|---|---|---|---|---|---|---|
| 5 | 0.026 | 0.091 | 0.088 | 0.078 | 0.018 | 0.014 | 0.014 | 0.028 | 0.045 |
| 6 | 0.066 | 0.270 | 0.294 | 0.113 | 0.158 | 0.062 | 0.048 | 0.087 | 0.137 |
| 7 | 0.096 | 0.350 | 0.398 | 0.217 | 0.198 | 0.270 | 0.092 | 0.140 | 0.220 |
| 8 | 0.182 | 0.270 | 0.643 | 0.214 | 0.277 | 0.172 | 0.250 | 0.173 | 0.273 |
| 9 | 0.206 | 0.509 | 0.506 | 0.269 | 0.250 | 0.220 | 0.176 | 0.184 | 0.290 |
| 10 | 0.206 | 0.509 | 0.506 | 0.269 | 0.250 | 0.220 | 0.176 | 0.184 | 0.290 |
| 11 | 0.201 | 0.330 | 0.371 | 0.283 | 0.268 | 0.316 | 0.315 | 0.185 | 0.284 |
| 12 | 0.226 | 0.309 | 0.395 | 0.117 | 0.203 | 0.086 | 0.708 | 0.504 | 0.319 |
| 13+ | 0.226 | 0.309 | 0.395 | 0.117 | 0.203 | 0.086 | 0.708 | 0.504 | 0.319 |
| Ave | 0.201 | 0.360 | 0.376 | 0.132 | 0.187 | 0.172 | 0.217 | 0.172 | |

Table 5. Estimates of F for widow rockfish by age and year, obtained by catch-at-age analysis with lambda - 0.01.

M - 0.15

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | Ave |
|---|---|---|---|---|---|---|---|---|---|
| 5 | 0.035 | 0.084 | 0.112 | 0.056 | 0.054 | 0.043 | 0.049 | 0.061 | 0.062 |
| 6 | 0.108 | 0.255 | 0.342 | 0.171 | 0.166 | 0.131 | 0.149 | 0.187 | 0.189 |
| 7 | 0.168 | 0.395 | 0.531 | 0.265 | 0.258 | 0.204 | 0.230 | 0.291 | 0.293 |
| 8 | 0.193 | 0.457 | 0.613 | 0.306 | 0.297 | 0.236 | 0.266 | 0.336 | 0.338 |
| 9 | 0.196 | 0.463 | 0.622 | 0.311 | 0.302 | 0.239 | 0.270 | 0.340 | 0.343 |
| 10 | 0.210 | 0.496 | 0.667 | 0.333 | 0.323 | 0.256 | 0.289 | 0.365 | 0.367 |
| 11 | 0.210 | 0.495 | 0.666 | 0.332 | 0.323 | 0.256 | 0.289 | 0.364 | 0.367 |
| 12 | 0.174 | 0.412 | 0.553 | 0.276 | 0.268 | 0.212 | 0.240 | 0.303 | 0.305 |
| 13+ | 0.055 | 0.129 | 0.173 | 0.086 | 0.084 | 0.067 | 0.075 | 0.095 | 0.095 |

M - 0.20

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | Ave |
|---|---|---|---|---|---|---|---|---|---|
| 5 | 0.029 | 0.069 | 0.091 | 0.045 | 0.045 | 0.037 | 0.043 | 0.057 | 0.052 |
| 6 | 0.090 | 0.213 | 0.280 | 0.139 | 0.138 | 0.113 | 0.133 | 0.175 | 0.160 |
| 7 | 0.140 | 0.332 | 0.435 | 0.216 | 0.214 | 0.176 | 0.207 | 0.271 | 0.249 |
| 8 | 0.159 | 0.378 | 0.496 | 0.246 | 0.244 | 0.200 | 0.235 | 0.309 | 0.283 |
| 9 | 0.157 | 0.373 | 0.489 | 0.243 | 0.241 | 0.198 | 0.232 | 0.305 | 0.280 |
| 10 | 0.160 | 0.381 | 0.500 | 0.248 | 0.246 | 0.202 | 0.238 | 0.312 | 0.286 |
| 11 | 0.150 | 0.357 | 0.469 | 0.233 | 0.231 | 0.190 | 0.223 | 0.292 | 0.268 |
| 12 | 0.118 | 0.281 | 0.369 | 0.183 | 0.182 | 0.149 | 0.175 | 0.230 | 0.211 |
| 13+ | 0.052 | 0.123 | 0.161 | 0.080 | 0.080 | 0.065 | 0.077 | 0.101 | 0.092 |

obtain estimates of F that were somewhat independent of the cohort analysis and the estimate of effort is dependent on the cohort analysis, we decided to set lambda at a lower value than in the 1987 assessment. Experimentation with lower values of lambda revealed that results were not very sensitive to reductions in lambda below 0.01, but that there were large changes when lambda is reduced from 0.5 to 0.1 and sometimes when lambda is reduced from 0.1 to 0.01. The results were also consistent with a significant decrease between 1982 and 1983. Fish aged 13 and older were included as a pooled age group.

We used the same age-structured simulation model used in earlier assessments and made the following assumptions regarding recruitment into the fishery:

1) For the average recruitment case, we assumed that the 1983 and subsequent year classes are equal in size to the average of the 1968 to 1982 cohorts.

2) For the survey recruitment case, recruitment for year classes after 1983 were based on a juvenile rockfish survey off the Central California coast. A mid water trawl survey has been conducted during May-June since 1983. Sample design was changed between 1983 and 1986, but it is thought that the changes were not sufficient to obscure major differences in juvenile rockfish abundance. Annual averages were standardized by dividing by the 1983-1987 average. The standardized annual averages were then multiplied by the average recruitment from the cohort and catch-at-age analyses to produce estimates of abundance for the 1983-1987 year classes. This assumes that densities of juvenile rockfish off Central California are proportional to year class strength. Also it is assumed that the 1983-1987 average year class strength is equal to the 1968-1982 average. The 1988 year class was assumed to be equal to the long term average.

3) For the density-dependent case, recruitment was assumed to be determined by a Beverton-Holt relationship. The parameters were obtained by assuming that recruitment would be reduced by 10 percent if spawning stock was reduced to 50 percent of the unfished level ($R_{0.5}/R_{1.0}=0.90$). Spawning stock estimates were obtained from the stock reconstruction analyses.

Number-at-age vectors at the start of 1989 were obtained as follows. The two stock reconstruction techniques provided estimates of the number-at-age vector at the beginning of 1987. Estimates of F-at-age in 1987 were used to project the number of fish ages 6 through 13+ present at the start of 1988. Recruitment in 1988 was obtained using the above assumptions about the strength of the 1983 year class. We then solved iteratively for the fishing mortality rates needed to obtain a 1988 harvest of 12,100 mt, using a selectivity curve obtained from the mean F-at-age vector (cohort analysis) or the least squares fit (catch-at-age analysis). Recruitment in 1989 was obtained using the above assumptions about the strength of the 1984 year class.

We used two approaches to develop harvest recommendations for 1989. The first approach was to maintain F at the level estimated to produce MSY. The second approach was to maintain yield at a constant level.

## RESULTS

The results of cohort and catch-at-analyses differed considerably. Estimates of age-specific F's for 1980-1986 from catch-at-age analysis were similar to the 1987 assessment, except that estimates of F for 13+ fish were lower. Estimates of age-specific F's from the cohort analysis tended to be lower for the 1979-81 year classes than the 1987 assessment. Results of the cohort analysis indicated that F increased for some ages between 1986 and 1987 and decreased for others, Table 4. The weighted average F decreased 26 percent between 1986 and 1987 when M=0.15 and 21% when M=0.20. Interpretation of changes in weighted average F is examined in the discussion section. Results of the catch-at-age analysis indicate that F-at-age increased 26% between 1986 and 1987 when M=0.15 and 21% when M=0.20. Estimates of abundance of recent year classes reflect the differences in F, Table 6 and 7. Catch-at-age analysis estimates of abundance of fish less than 9 years in 1987 are much less than estimates from cohort analysis. The different estimates of young fish are sufficient to cause major differences in estimates of biomass, Table 8. Biomass in 1987 was estimated to be almost as high as 1980 by cohort analysis and only 35-40% of the 1980 biomass by catch-at-age analysis.

Both methods indicate that the 1977-1981 year classes are strong compared to the 1972-1976 year classes, Figure 4. The cohort analysis indicate that the 1980 year class is stronger or almost as strong as the 1970 year class and much stronger than the 1978 year class. The catch-at-age analysis indicates that the 1980 year class is less than half the size of the 1970 year class and about the same size as the 1978 year class. Based on cohort analysis, average recruitment was 29.6 and 34.2 million fish for M = 0.15 and M = 0.20 respectively. Estimates of average recruitment from catch-at-age analysis were 20.8 and 31.1 million fish for M = 0.15 and M = 0.20 respectively.

Estimated selectivity patterns from cohort and catch-at-age analysis were similar for fish ages 5-11 (Figure 5). The pattern derived from catch-at-age analysis indicates sharply lower vulnerability for fish ages 12 and older. A similar result was obtained from cohort analysis in the 1986 assessment, but not the 1987 assessment. The current cohort analysis predicts only slightly reduced vulnerability for older fish, due apparently to the relatively large estimated landings of 11- and 12-year-old fish and 12-year-old fish in 1987 (Table 2). It should be noted that the cohort analysis assumes that F is constant for fish older than

Table 6. Estimates of population size (millions of fish) of widow rockfish by age and year, obtained by cohort analysis.

M = 0.15

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|---|---|
| 5 | 11.1 | 7.7 | 30.6 | 30.8 | 31.8 | 79.5 | 55.8 | 21.5 |
| 6 | 6.9 | 9.3 | 5.9 | 23.9 | 24.4 | 26.9 | 67.6 | 47.4 |
| 7 | 4.8 | 5.5 | 5.9 | 3.7 | 18.3 | 17.9 | 21.9 | 55.8 |
| 8 | 5.3 | 3.7 | 3.3 | 3.3 | 2.6 | 12.9 | 11.9 | 17.4 |
| 9 | 18.9 | 3.7 | 2.4 | 1.4 | 2.3 | 1.7 | 9.4 | 8.2 |
| 10 | 29.5 | 13.0 | 1.9 | 1.2 | 0.9 | 1.5 | 1.2 | 7.0 |
| 11 | 12.3 | 20.2 | 6.4 | 0.9 | 0.8 | 0.6 | 1.1 | 0.9 |
| 12 | 8.8 | 8.5 | 12.2 | 3.7 | 0.6 | 0.5 | 0.4 | 0.7 |
| 13+ | 17.4 | 16.3 | 25.1 | 30.9 | 16.3 | 19.0 | 3.1 | 4.2 |

M = 0.20

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|---|---|
| 5 | 12.9 | 8.7 | 34.0 | 33.2 | 31.9 | 75.3 | 50.8 | 18.9 |
| 6 | 7.9 | 10.3 | 6.5 | 25.5 | 25.1 | 25.6 | 60.9 | 41.0 |
| 7 | 5.5 | 6.0 | 6.4 | 4.0 | 18.7 | 17.6 | 19.7 | 47.5 |
| 8 | 6.0 | 4.1 | 3.5 | 3.5 | 2.6 | 12.5 | 11.0 | 14.7 |
| 9 | 21.1 | 4.1 | 2.6 | 1.5 | 2.3 | 1.6 | 8.6 | 7.0 |
| 10 | 33.0 | 14.1 | 2.0 | 1.3 | 0.9 | 1.5 | 1.1 | 5.9 |
| 11 | 13.5 | 22.0 | 6.9 | 1.0 | 0.8 | 0.6 | 1.0 | 0.7 |
| 12 | 9.1 | 9.0 | 12.9 | 3.9 | 0.6 | 0.5 | 0.4 | 0.6 |
| 13+ | 17.8 | 17.3 | 26.6 | 32.4 | 16.6 | 18.6 | 2.8 | 3.5 |

Table 7. Estimates of population size (millions of fish) of widow rockfish by age and year, obtained by catch-at-age analysis with lambda = 0.01.

M = 0.15

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|---|---|
| 5 | 11.4 | 6.5 | 23.3 | 27.9 | 14.1 | 28.3 | 18.3 | 8.6 |
| 6 | 7.4 | 9.5 | 5.2 | 18.0 | 22.7 | 11.5 | 23.3 | 15.0 |
| 7 | 4.2 | 5.7 | 6.3 | 3.2 | 13.0 | 16.6 | 8.7 | 17.3 |
| 8 | 5.0 | 3.1 | 3.3 | 3.2 | 2.1 | 8.7 | 11.6 | 5.9 |
| 9 | 15.1 | 3.5 | 1.7 | 1.5 | 2.0 | 1.3 | 5.9 | 7.7 |
| 10 | 28.3 | 10.7 | 1.9 | 0.8 | 1.0 | 1.3 | 0.9 | 3.9 |
| 11 | 11.9 | 19.7 | 5.6 | 0.8 | 0.5 | 0.6 | 0.9 | 0.6 |
| 12 | 12.3 | 8.3 | 10.3 | 2.5 | 0.5 | 0.3 | 0.4 | 0.6 |
| 13+ | 51.4 | 50.8 | 43.2 | 36.4 | 30.3 | 24.4 | 19.8 | 16.1 |

M = 0.20

| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|---|---|
| 5 | 14.3 | 8.2 | 29.4 | 35.0 | 17.3 | 33.6 | 21.1 | 9.5 |
| 6 | 9.0 | 11.4 | 6.2 | 22.0 | 27.4 | 13.6 | 26.5 | 16.5 |
| 7 | 5.1 | 6.7 | 7.5 | 3.9 | 15.7 | 19.5 | 9.9 | 19.0 |
| 8 | 6.0 | 3.6 | 3.9 | 4.0 | 2.5 | 10.4 | 13.4 | 6.6 |
| 9 | 18.7 | 4.2 | 2.0 | 2.0 | 2.5 | 1.6 | 6.9 | 8.7 |
| 10 | 36.7 | 13.1 | 2.4 | 1.0 | 1.3 | 1.6 | 1.1 | 4.5 |
| 11 | 16.5 | 25.6 | 7.3 | 1.2 | 0.7 | 0.8 | 1.1 | 0.7 |
| 12 | 17.7 | 11.6 | 14.7 | 3.8 | 0.8 | 0.4 | 0.5 | 0.7 |
| 13+ | 55.8 | 56.2 | 47.9 | 41.7 | 34.0 | 26.3 | 20.4 | 15.9 |

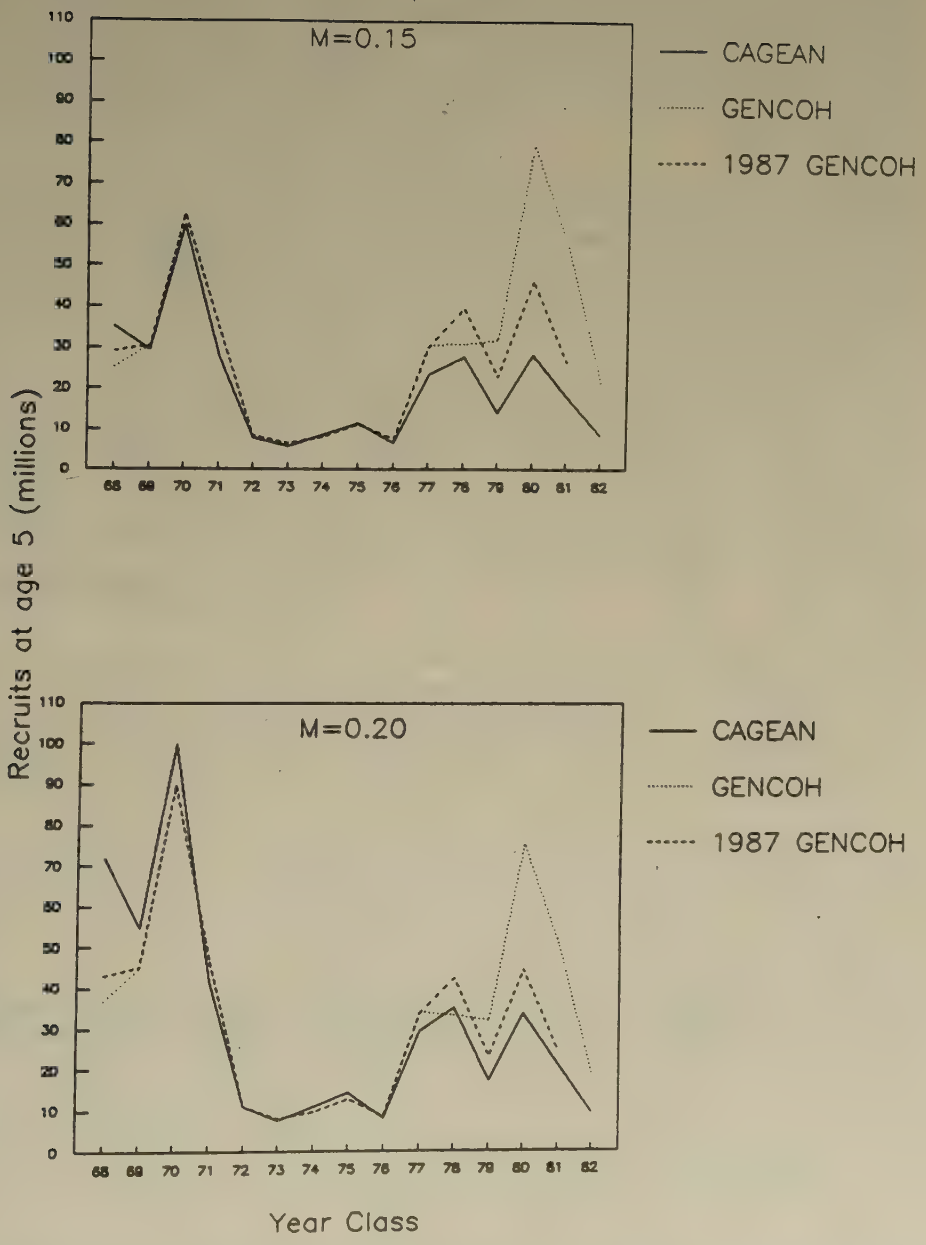

Figure 4. Estimates of widow rockfish recruitment at age 5 obtained from cohort (GENCOH) and catch-at-age analysis (CAGEAN). Estimates from the 1987 assessment (1987 GENCOH) are included for comparison.

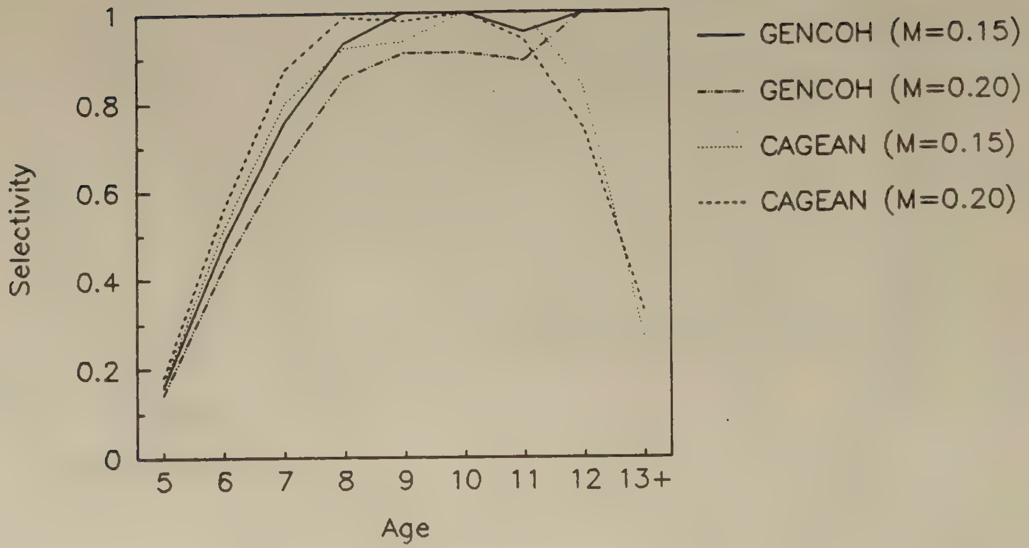

**Figure 5.** Estimates of age-specific selectivity for widow rockfish obtained by cohort (GENCOH) and catch-at-age analysis (CAGEAN) at two levels of natural mortality.

12 years. The 1986 catch of age-12 fish had a particularly great impact on the results because the starting value for the entire analysis is for the same cohort. Because $F_{10}(1984)$ (and therefore $N_{10}(1984)$) is fixed, a large catch from that cohort two years later is attributed to a high rate of fishing mortality. The unusually high $F_{12}(1986)$ and $F_{12}(1987)$ produce a low estimates of $N_{13+}(1986)$ and $N_{13+}(1987)$ because $N_{13+}$ is estimated as $C_{13+}/u_{12}$ under the assumption that the exploitation rate is equal for fish ages 12 and older.

Estimates from catch-at-age analysis were less effected by the 1986 catch of older fish because of the structure imposed by the constant selectivity assumption. In addition in catch-at-age analysis the catch of age 13+ fish must be partially supported by the survivors of exploitation of 12-year-old fish. The disadvantage is that if a change in fishing patterns occurred in 1986 and 1987, it would not be accurately represented by the catch-at-age analysis. The model can be fitted to catch data from two or more periods where selectivity patterns differed. That assumption was not used here, however, because the high catch of older fish in 1986 may be simply a random event or due to sampling error or errors in aging. Either possibility would cause cohort analysis to underestimate the number of age-13+ fish and stock biomass. An additional effect of the high $F_{12}(1986)$ in the cohort analysis is that estimates of $F_{12}(1980)$ are substantially higher than estimates in the 1986 assessment. This change results in a lower estimate of $N_{12}(1980)$, which is used to estimate the size of the 1968 year class (Figure 4).

While estimates of biomass from the cohort analysis indicate little trend, estimates from the catch-at-age analysis indicate that biomass in 1987 is less than 40 percent of 1980 levels, Figure 6. The cohort analysis results indicate that the biomass of fish less than 13 years old increased since 1980. Results from the catch-at-age analysis indicate that biomass of young fish decreased by more than 50 percent.

Equilibrium yield curves from cohort and catch-at-age analysis were similar to each other and to curves obtained in the 1987 assessment. It appears that when $M = 0.15$ an F of 0.25 for fully recruited fish (age 9) provides about the maximum yield if a stock-recruitment relationship exists and does not extract a large penalty if no relationship exists (Figures 7-8). When $M = 0.20$ the appropriate value of F is 0.30. Assuming that MSY would be obtained at that level of effort, estimates of MSY from cohort analysis results range from 8,200 to 13,300 mt, with an average of 10,700 mt. Biomass at MSY ranges from 54,300 mt to 87,800 mt with an average of 70,500 mt. Using results of catch-at-age analysis, estimates of MSY ranged from 5,900 to 11,400 mt, with an average of 8,400 mt. Biomass at MSY ranged from 45,400 mt to 72,500 mt with an average of 57,900 mt. The average of all estimates of MSY was 9,500 mt. The stock appears to be at or above the MSY level, Table 8.

Equilibrium yield curves provide an indication of the average productivity of a stock; however, they fail to account for the short-term effects of variations in year class strength. We used a constant

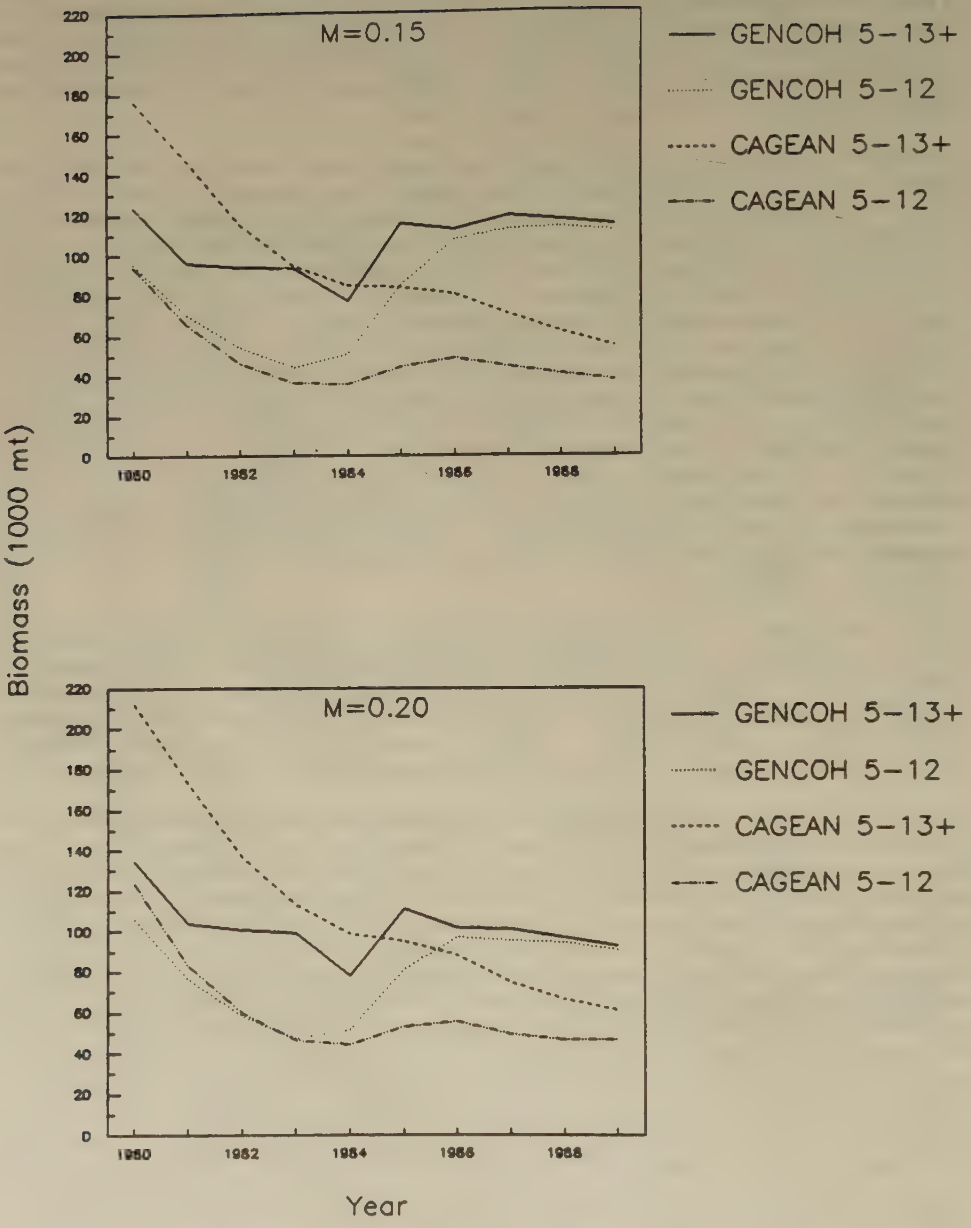

Figure 6. Estimates of widow rockfish biomasss obtained by cohort (GENCOH) and catch-at-age analysis (CAGEAN) at two levels of natural mortality.

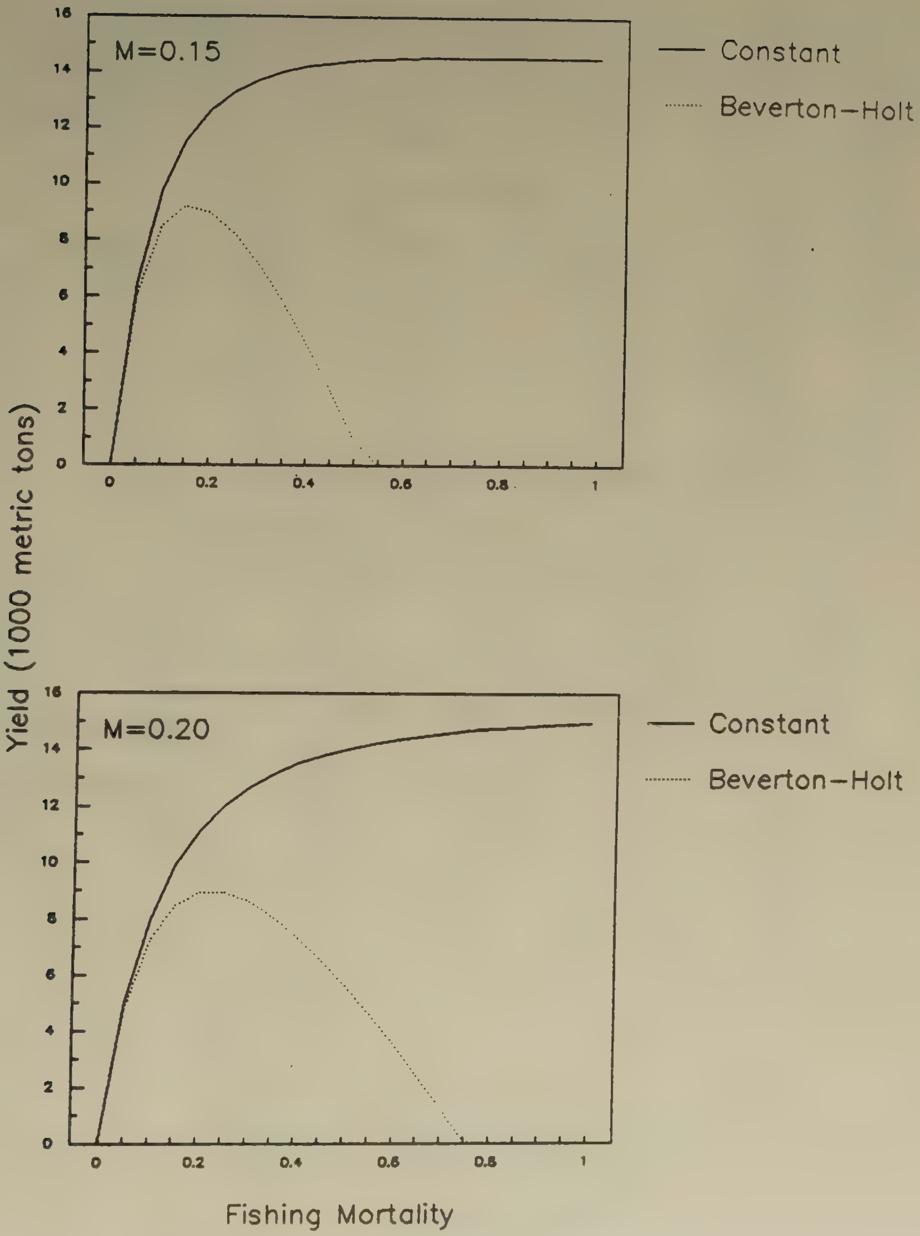

Figure 7. Estimates of equilibrium yield for widow rockfish based on results from cohort analysis.

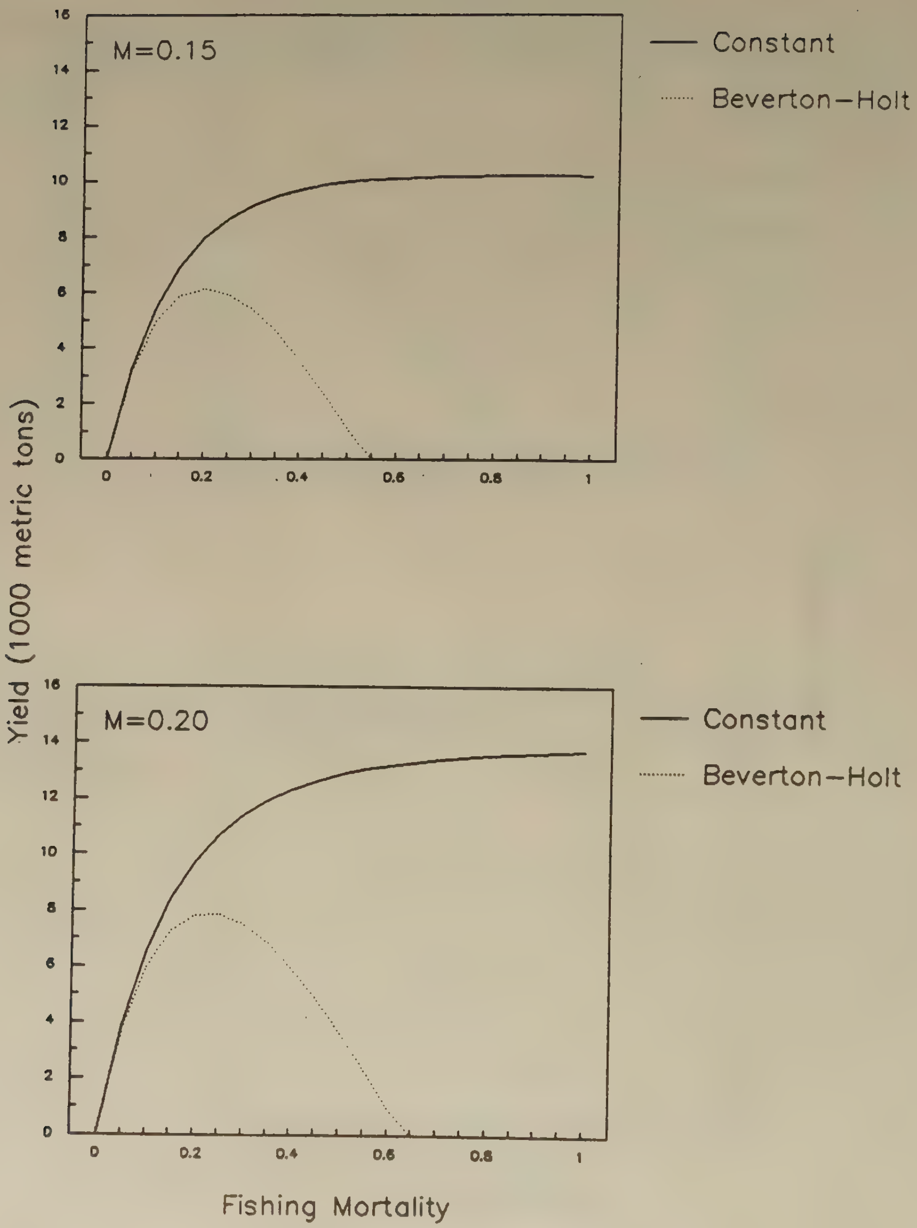

Figure 8. Estimates of equilibrium yield for widow rockfish based on results from catch-at-age analysis.

Table 8. Estimates from cohort (GENCOH) and catch-at-age (CAGEAN) analysis of widow rockfish biomass (older than 4) and population fecundity from 1980 through 1989. Estimates for 1988 and 1989 from the current assessment (88 GENCOH and 88 CAGEAN) are averages for three recruitment cases, using projected number-at-age vectors. Similar bimass projections were made for 1987 and 1988 in the 1987 assessment (87 GENCOH).

Biomass (1000 mt)

| Year | M = 0.15 | | | M = 0.20 | | |
|---|---|---|---|---|---|---|
| | 87 GENCOH | 88 GENCOH | 88 CAGEAN | 87 GENCOH | 88 GENCOH | 88 CAGEAN |
| 1980 | 129.2 | 123.2 | 176.3 | 141.2 | 134.4 | 212.7 |
| 1981 | 96.4 | 96.0 | 146.7 | 104.1 | 103.8 | 173.2 |
| 1982 | 93.9 | 94.1 | 115.2 | 100.8 | 100.9 | 136.3 |
| 1983 | 97.6 | 93.4 | 94.7 | 103.3 | 98.9 | 113.2 |
| 1984 | 76.7 | 76.8 | 84.5 | 77.9 | 78.0 | 98.5 |
| 1985 | 98.4 | 115.1 | 83.4 | 95.3 | 111.0 | 94.9 |
| 1986 | 80.3 | 112.0 | 79.8 | 73.0 | 101.6 | 88.2 |
| 1987 | 80.8 | 118.5 | 70.0 | 72.5 | 101.2 | 74.7 |
| 1988 | 74.0 | 116.7 | 61.4 | 65.9 | 97.3 | 66.4 |
| 1989 | | 114.3 | 54.0 | | 92.9 | 61.5 |

Population Fecundity (billion oocytes)

| Year | M = 0.15 | | M = 0.20 | |
|---|---|---|---|---|
| | GENCOH | CAGEAN | GENCOH | CAGEAN |
| 1980 | 421.4 | 660.0 | 454.8 | 788.7 |
| 1981 | 330.7 | 560.5 | 355.8 | 657.0 |
| 1982 | 302.7 | 414.7 | 321.7 | 485.0 |
| 1983 | 268.8 | 297.7 | 282.8 | 349.9 |
| 1984 | 165.8 | 253.8 | 168.5 | 290.2 |
| 1985 | 209.8 | 228.2 | 204.9 | 253.0 |
| 1986 | 130.9 | 209.9 | 119.3 | 225.8 |
| 1987 | 203.6 | 196.2 | 172.3 | 205.2 |
| 1988 | 253.6 | 173.7 | 201.5 | 176.4 |
| 1989 | 287.2 | 143.5 | 211.5 | 141.9 |

effort policy with $F_9 = 0.25$ when $M = 0.15$ and $F_9 = 0.30$ when $M = 0.20$ to forecast yields from 1989 to 1993, starting from the estimated number-at-age vector for 1988 (Table 9). The average yield would be 7,500 to 18,100 mt in 1989 and 7,800 to 16,300 mt in 1990, with an average of 17,200 mt from cohort analysis and 7,600 from catch-at-age analysis. The estimate from cohort analysis is 42% higher than the 1987 ABC and OY, while the estimate from catch-at-age analysis is 38% lower. The cohort analysis predicts a reduction in yield through 1993. The catch-at-age analysis predicts increases in yield through 1993.

Another approach for evaluating the short-term effects of variations in year class strength is to determine the sequence of fishing mortality rates needed to maintain a constant harvest. Using results from the analyses, we determined the levels of fishing mortality needed to produce constant yields of 9,000 to 15,000 mt (Table 10). Under the results of the cohort analysis, yields of 12,000 to 13,000 mt (the average yield under a constant effort policy) could be taken in 1988 and 1989, with slight increases in F after 1989, and F would be about 0.2 which is close to the F that would produce MSY under the density dependent recruitment assumption, Figure 7. Under the catch at age results F would be about 0.5, tend to increase and would eventually reduce equilibrium yields to a small fraction of MSY under the dependent recruitment assumption, Figure 8. If yields are held at the MSY level (9,500 mt), results of the cohort analysis indicated that F would be about 0.15, tend to decrease and be close to the MSY level under the density dependent recruitment assumption. Under the results of catch-at-age analysis F would be about 0.4 and tend to decrease unless the density dependent recruitment assumption is true and $M=0.15$.

## DISCUSSION

The conflicting results of cohort and catch-at-age analysis verify that catch-at-age data alone do not provide sufficient data to estimate fishing mortality and population size. This is particularly true for recent year classes. Two constraints were placed on the cohort analysis. Fishing mortality of age 9 and 10 year old fish was assumed to be equal. Results of the catch-at-age analysis indicated that the assumption is reasonable. It was also assumed that fishing mortality dropped substantially between 1982 and 1983, because of regulations implemented in 1983. The choice of $F_9(1984) = 0.25$ was originally made in the 1985 assessment because it resulted in about a 50 percent drop in the sum of F over age from 1982 to 1983. Estimates of F for younger ages in 1982 and 1983 have changed since the 1985 assessment as additional data became available. It now appears that F dropped more than 50 percent between 1982 and 1983; although not for every age group. When $F_9(1984)$ was set to 0.30 unrealistically high values of F were estimated for older aged fish.

Average F for a year may be estimated in a variety of ways. We believe that average F from the cohort analysis should be weighted by catch at age (in numbers) for the purpose of estimating fishing effort for CAGEAN because of the estimation procedure. The weighted average F can change

Table 9. Estimated yield (thousands of metric tons) when F for fully recruited fish is 0.25 for M = 0.15 and 0.30 for M = 0.20 and three assumptions about recruitment.

Cohort Analysis

| | Recruitment | | | | | | |
|---|---|---|---|---|---|---|---|
| | Average | | Survey | | Beverton-Holt | | Average |
| Year | M=0.15 | M=0.20 | M=0.15 | M=0.20 | M=0.15 | M=0.20 | |
| 1989 | 20.7 | 17.1 | 18.8 | 14.9 | 20.3 | 16.8 | 18.1 |
| 1990 | 18.9 | 15.5 | 17.0 | 13.5 | 18.0 | 14.9 | 16.3 |
| 1991 | 17.3 | 14.6 | 16.4 | 13.8 | 15.8 | 13.5 | 15.2 |
| 1992 | 16.3 | 14.1 | 16.1 | 14.2 | 14.3 | 12.5 | 14.6 |
| 1993 | 15.7 | 13.7 | 16.7 | 14.9 | 13.3 | 11.8 | 14.4 |
| Average | 17.8 | 15.0 | 17.0 | 14.3 | 16.3 | 13.9 | 15.7 |

Average for 1988 and 1989 (estimate of ABC): 17.2

Catch-at-Age Analysis

| | Recruitment | | | | | | |
|---|---|---|---|---|---|---|---|
| | Average | | Survey | | Beverton-Holt | | Average |
| Year | M=0.15 | M=0.20 | M=0.15 | M=0.20 | M=0.15 | M=0.20 | |
| 1989 | 6.9 | 9.5 | 5.5 | 7.0 | 6.7 | 9.5 | 7.5 |
| 1990 | 7.1 | 9.7 | 5.8 | 7.7 | 6.8 | 9.8 | 7.8 |
| 1991 | 7.5 | 10.3 | 7.1 | 10.1 | 7.0 | 10.5 | 8.8 |
| 1992 | 7.9 | 10.8 | 8.0 | 11.4 | 7.2 | 11.0 | 9.4 |
| 1993 | 8.1 | 11.1 | 8.7 | 12.3 | 7.2 | 11.2 | 9.8 |
| Average | 7.5 | 10.3 | 7.0 | 9.7 | 7.0 | 10.4 | 8.7 |

Average for 1988 and 1989 (estimate of ABC): 7.6

Table 10. Estimated F for fully recruited fish needed to maintain harvests of 9,000 to 15,000 mt for two values of M and three assumptions about recruitment.

| | | Cohort Analysis Recruitment | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Target harvest | | Average | | Survey | | Beverton-Holt | | |
| | Year | M=0.15 | M=0.20 | M=0.15 | M=0.20 | M=0.15 | M=0.20 | Average |
| 9,000 | 1989 | 0.10 | 0.15 | 0.11 | 0.17 | 0.10 | 0.15 | 0.13 |
| | 1990 | 0.10 | 0.15 | 0.11 | 0.17 | 0.10 | 0.15 | 0.13 |
| | 1991 | 0.10 | 0.15 | 0.11 | 0.16 | 0.11 | 0.16 | 0.13 |
| | 1992 | 0.09 | 0.14 | 0.10 | 0.15 | 0.11 | 0.16 | 0.12 |
| | 1993 | 0.09 | 0.14 | 0.09 | 0.13 | 0.11 | 0.16 | 0.12 |
| 10,000 | 1989 | 0.11 | 0.17 | 0.13 | 0.19 | 0.12 | 0.17 | 0.15 |
| | 1990 | 0.11 | 0.17 | 0.13 | 0.20 | 0.12 | 0.18 | 0.15 |
| | 1991 | 0.11 | 0.17 | 0.12 | 0.19 | 0.12 | 0.18 | 0.15 |
| | 1992 | 0.11 | 0.16 | 0.12 | 0.17 | 0.12 | 0.19 | 0.15 |
| | 1993 | 0.11 | 0.16 | 0.11 | 0.16 | 0.13 | 0.19 | 0.14 |
| 11,000 | 1989 | 0.13 | 0.19 | 0.14 | 0.21 | 0.13 | 0.19 | 0.16 |
| | 1990 | 0.12 | 0.19 | 0.14 | 0.22 | 0.13 | 0.20 | 0.17 |
| | 1991 | 0.13 | 0.19 | 0.14 | 0.21 | 0.14 | 0.21 | 0.17 |
| | 1992 | 0.12 | 0.19 | 0.13 | 0.20 | 0.14 | 0.21 | 0.16 |
| | 1993 | 0.12 | 0.18 | 0.12 | 0.18 | 0.15 | 0.22 | 0.16 |
| 12,000 | 1989 | 0.14 | 0.20 | 0.15 | 0.24 | 0.14 | 0.21 | 0.18 |
| | 1990 | 0.14 | 0.21 | 0.16 | 0.25 | 0.15 | 0.22 | 0.19 |
| | 1991 | 0.14 | 0.21 | 0.15 | 0.24 | 0.15 | 0.23 | 0.19 |
| | 1992 | 0.14 | 0.21 | 0.15 | 0.23 | 0.16 | 0.25 | 0.19 |
| | 1993 | 0.14 | 0.21 | 0.14 | 0.21 | 0.17 | 0.26 | 0.19 |
| 13,000 | 1989 | 0.15 | 0.22 | 0.17 | 0.26 | 0.15 | 0.23 | 0.20 |
| | 1990 | 0.15 | 0.23 | 0.17 | 0.28 | 0.16 | 0.24 | 0.20 |
| | 1991 | 0.16 | 0.24 | 0.17 | 0.27 | 0.17 | 0.26 | 0.21 |
| | 1992 | 0.16 | 0.24 | 0.17 | 0.26 | 0.18 | 0.28 | 0.22 |
| | 1993 | 0.16 | 0.25 | 0.16 | 0.24 | 0.19 | 0.30 | 0.22 |
| 14,000 | 1989 | 0.16 | 0.24 | 0.18 | 0.28 | 0.17 | 0.25 | 0.21 |
| | 1990 | 0.17 | 0.26 | 0.19 | 0.31 | 0.18 | 0.27 | 0.23 |
| | 1991 | 0.17 | 0.27 | 0.19 | 0.30 | 0.19 | 0.30 | 0.24 |
| | 1992 | 0.18 | 0.28 | 0.19 | 0.30 | 0.21 | 0.32 | 0.25 |
| | 1993 | 0.18 | 0.28 | 0.18 | 0.28 | 0.22 | 0.36 | 0.25 |
| 15,000 | 1989 | 0.18 | 0.26 | 0.19 | 0.30 | 0.18 | 0.26 | 0.23 |
| | 1990 | 0.18 | 0.28 | 0.21 | 0.34 | 0.19 | 0.29 | 0.25 |
| | 1991 | 0.19 | 0.30 | 0.21 | 0.34 | 0.21 | 0.33 | 0.26 |
| | 1992 | 0.20 | 0.31 | 0.21 | 0.33 | 0.23 | 0.37 | 0.28 |
| | 1993 | 0.20 | 0.33 | 0.20 | 0.32 | 0.25 | 0.42 | 0.29 |

Table 10. Continued

| | | Catch-at-Age-Analysis | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Recruitment | | | | | | |
| Target harvest | | Average | | Survey | | Beverton-Holt | | |
| | Year | M=0.15 | M=0.20 | M=0.15 | M=0.20 | M=0.15 | M=0.20 | Average |
| 9,000 | 1989 | 0.34 | 0.28 | 0.44 | 0.40 | 0.34 | 0.28 | 0.35 |
| | 1990 | 0.34 | 0.27 | 0.46 | 0.38 | 0.36 | 0.27 | 0.35 |
| | 1991 | 0.34 | 0.25 | 0.38 | 0.28 | 0.37 | 0.25 | 0.31 |
| | 1992 | 0.33 | 0.23 | 0.34 | 0.24 | 0.38 | 0.23 | 0.29 |
| | 1993 | 0.33 | 0.22 | 0.31 | 0.21 | 0.39 | 0.22 | 0.28 |
| 10,000 | 1989 | 0.38 | 0.32 | 0.49 | 0.46 | 0.39 | 0.32 | 0.39 |
| | 1990 | 0.40 | 0.31 | 0.53 | 0.44 | 0.42 | 0.31 | 0.40 |
| | 1991 | 0.40 | 0.29 | 0.45 | 0.33 | 0.45 | 0.29 | 0.37 |
| | 1992 | 0.40 | 0.28 | 0.42 | 0.28 | 0.47 | 0.27 | 0.35 |
| | 1993 | 0.41 | 0.27 | 0.39 | 0.25 | 0.51 | 0.26 | 0.35 |
| 11,000 | 1989 | 0.42 | 0.35 | 0.55 | 0.51 | 0.43 | 0.36 | 0.44 |
| | 1990 | 0.46 | 0.36 | 0.62 | 0.50 | 0.48 | 0.35 | 0.46 |
| | 1991 | 0.48 | 0.34 | 0.54 | 0.38 | 0.53 | 0.33 | 0.43 |
| | 1992 | 0.49 | 0.33 | 0.51 | 0.33 | 0.59 | 0.32 | 0.43 |
| | 1993 | 0.51 | 0.32 | 0.49 | 0.30 | 0.66 | 0.31 | 0.43 |
| 12,000 | 1989 | 0.47 | 0.39 | 0.62 | 0.57 | 0.48 | 0.39 | 0.49 |
| | 1990 | 0.52 | 0.40 | 0.71 | 0.57 | 0.56 | 0.40 | 0.53 |
| | 1991 | 0.56 | 0.39 | 0.63 | 0.43 | 0.63 | 0.39 | 0.50 |
| | 1992 | 0.61 | 0.39 | 0.63 | 0.39 | 0.73 | 0.37 | 0.52 |
| | 1993 | 0.65 | 0.38 | 0.62 | 0.36 | 0.87 | 0.37 | 0.54 |
| 13,000 | 1989 | 0.52 | 0.43 | 0.69 | 0.63 | 0.53 | 0.43 | 0.54 |
| | 1990 | 0.59 | 0.45 | 0.82 | 0.65 | 0.63 | 0.45 | 0.60 |
| | 1991 | 0.67 | 0.45 | 0.74 | 0.50 | 0.76 | 0.44 | 0.59 |
| | 1992 | 0.75 | 0.46 | 0.77 | 0.46 | 0.93 | 0.44 | 0.64 |
| | 1993 | 0.85 | 0.46 | 0.81 | 0.43 | 1.20 | 0.44 | 0.70 |
| 14,000 | 1989 | 0.56 | 0.47 | 0.76 | 0.69 | 0.58 | 0.47 | 0.59 |
| | 1990 | 0.67 | 0.51 | 0.94 | 0.73 | 0.72 | 0.50 | 0.68 |
| | 1991 | 0.79 | 0.52 | 0.86 | 0.57 | 0.91 | 0.51 | 0.69 |
| | 1992 | 0.93 | 0.54 | 0.96 | 0.54 | 1.19 | 0.52 | 0.78 |
| | 1993 | 1.13 | 0.55 | 1.07 | 0.51 | 1.74 | 0.54 | 0.92 |
| 15,000 | 1989 | 0.61 | 0.51 | 0.83 | 0.76 | 0.63 | 0.51 | 0.64 |
| | 1990 | 0.76 | 0.56 | 1.07 | 0.82 | 0.82 | 0.56 | 0.77 |
| | 1991 | 0.93 | 0.60 | 1.01 | 0.64 | 1.09 | 0.58 | 0.81 |
| | 1992 | 1.18 | 0.63 | 1.22 | 0.64 | 1.58 | 0.61 | 0.98 |
| | 1993 | 1.57 | 0.67 | 1.49 | 0.62 | 2.78 | 0.65 | 1.30 |

between years even if the F at age vector remains constant. The strong 1977 and 1978 year classes recruited in 1982 and 1983. This tended to reduce the weighted average F in 1982 compared to 1981 and 1983 compared to 1982. Also the relative contribution of older fish decreased in 1983. This also tended to decrease the weighted average F in 1983 compared to 1982. When M = 0.15 if the observed 1982 age composition of the catch had occurred in 1981, the 1981 weighted average F would have been 0.318 instead of 0.387 as observed. If the observed 1983 age composition had occurred in 1982, the 1982 weighted average F would have been 0.346 instead of the observed 0.397.

Another measure of the impact of fishing on the stock is the exploitation rate in terms of biomass. This is calculated by dividing the catch in weight by the biomass. Exploitation rate is also estimated to have decreased by more than 50 percent between 1982 and 1983 by both cohort and catch-at-age analysis, Table 11. The lowest exploitation rate is estimated to have occurred in 1985, which is also the year of lowest catch since 1980 and the earliest date of restriction of the fishery to incidental catches. The cohort analysis indicates that exploitation rate increased to 1983 levels in 1987. The catch-at-age analysis indicates that exploitation rates increased to 1981 levels in 1987.

The number of vessels participating in the fishery for widow rockfish in Oregon (which is the center of the fishery) has doubled since 1982 and 1983 (J. Golden ODFW). However trip regulations are more restrictive. In 1983 there was no trip frequency limit. In 1987, only one trip per week was allowed. The season closed about a month latter in 1987 than in 1983. The number of Californian vessels participating in the fishery appeared to decrease between 1982-1983 and 1987.

It appears reasonable that fishing intensity in 1987 is as high or higher than 1983. It seems unlikely that it is as high as 1981, because of the regulations and apparent reduced effort in California. However, the increased number of vessels participating in the Oregon fishery could cause 1987 effort to be higher than 1983 effort.

At this time we believe that there is insufficient information to choose between the cohort and catch-at-age results. Since there is a great deal of uncertainty about the strength of recent year classes and these year classes are an important component of the stock, we recommend that ABC be set to the average estimate of MSY, 9,500 mt. The stock would continue to be able to support a 9,500 mt fishery in 1990 without a large increase in fishing mortality.

The strength of the important 1980 year class should be better established with an additional year of data. However, because of the lack of funding some areas were not adequately sampled in 1988. Thus there will be greater than usual uncertainty in the estimates of age composition for the 1988 landings. There is no reason to expect a much better estimate of the apparently strong 1981 year class than we now have for the 1980 year class. Thus unless additional information is

Table 11. Estimated rates of exploitation of widow rockfish age 5 and older in terms of biomass. Projections for 1988 and 1989 are as described in Table 8.

| | Cohort Analysis | | Catch-at-Age-Analysis | | |
|---|---|---|---|---|---|
| Year | M = 0.15 | M = 0.20 | M = 0.15 | M = 0.20 | Average |
| 1980 | 0.17 | 0.15 | 0.12 | 0.10 | 0.14 |
| 1981 | 0.29 | 0.27 | 0.19 | 0.16 | 0.23 |
| 1982 | 0.28 | 0.26 | 0.23 | 0.19 | 0.24 |
| 1983 | 0.11 | 0.10 | 0.11 | 0.09 | 0.10 |
| 1984 | 0.13 | 0.12 | 0.11 | 0.10 | 0.12 |
| 1985 | 0.08 | 0.08 | 0.11 | 0.09 | 0.09 |
| 1986 | 0.08 | 0.09 | 0.12 | 0.11 | 0.10 |
| 1987 | 0.10 | 0.12 | 0.17 | 0.16 | 0.14 |
| 1988 | 0.10 | 0.12 | 0.20 | 0.18 | 0.15 |
| 1989 | 0.11 | 0.13 | 0.23 | 0.20 | 0.17 |

used for the next analysis, there is likely to be continued uncertainty about the status of the stock.

We have begun exploring one additional source of information. The data indicate that there are fairly consistent differences in age composition among areas. It may be useful to develop an estimation procedure for the selectivity curve of the most recent year of data based on the area composition of the catch. This procedure would estimate changes in selectivity due to changes in the area composition of the catch. For example, catches from the North Columbia Area tend to be dominated by relatively young fish. If the proposed procedure had been applied, starting F's for young fish in 1987 probably would have been higher than those used in the cohort analysis of this report.

An additional source of information is the juvenile rockfish survey off of Central California. If the abundance of juvenile rockfish prove to be related to year class strength, the results of the survey can be used to tune the cohort analysis. The first year class (1983) covered by the survey began recruiting to the fishery as five-year-old fish in 1988. It will take a number of years to verify the utility of the survey results.

## LITERATURE CITED

Barss, W.H. and T. Wyllie Echeverria. 1987. Maturity of widow rockfish Sebastes entomelas from the Northeastern Pacific, 1977-82. In Lenarz, W.H. and D.R. Gunderson (eds.), Widow Rockfish, p. 13-18. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 48.

Boehlert, G.W., W.H. Barss, and P.B. Lamberson. 1982. Fecundity of the widow rockfish, Sebastes entomelas, off the coast of Oregon. Fish Bull., U.S. 80:881-884.

Deriso, R. B., T. J. Quinn II, and P. R. Neal. 1985. Catch-age analyis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 815-824.

Hightower, J. E., and W. H. Lenarz. 1987. Status of the widow rockfish fishery. (Document submitted to the Pacific Fisheries Management Council, Portland, Oregon, August, 1987). Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

Lenarz, W.H. 1987. Ageing and growth of widow rockfish. In Lenarz, W.H. and D.R. Gunderson (eds.), Widow Rockfish, p. 31-35. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 48.

Lenarz, W.H. and J.E. Hightower. 1985. Status of the widow rockfish fishery. (Document submitted to the Pacific Fisheries Managment Council, Portland, Oregon, October, 1985). Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

Murphy, G. 1965. A solution of the catch equation. J. Fish. Res. Bd. Can. 22:191-202.

Whipple, J.A. (ed.). MS. Progress in rockfish recruitment studies. To be published as a Southwest Fisheries Center Administrative Report.

Appendix I. Comments on 1987 stock assessment by a member of the SSC assigned to review the report.

To: GMT/SSC Groundfish Subgroup
From: David Hankin, SSC
Subject: Widow Rockfish stock report
Date: 1 October 1987

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At the last SSC meeting I was assigned the responsibility of review for the widow rockfish stock report. Because I will be unable to attend the meeting of 7 October, I'd like to ask that the following comments be considered by the GMT/SSC Subgroup.

At the outset, let me say that I was impressed with the report, especially by the attached tables and figures and with the apparent honesty with which the authors presented sometimes conflicting results. My comments below ought not to be construed as indicating that I think this report is unsound, and should be viewed as constructive or irrelevant criticisms.

1. As Bill Clark pointed out in the previous meeting, both cohort and catch-at-age analyses appear to hinge on choice of $F_9(1984)$ which is based on "forcing" a decline in average F of about 50% from 1982 to 1983, and about 10% from 1983 to 1984. I think the report should include some strong justification for this important assumption, or refer the reader to such in an earlier assessment document (which I don't have since I'm new at this). In addition, the report would have been stronger if there were some comparative results for choices of initial F that did not meet this assumption. I have no feeling for how important this assumption would be on the final stock assessment in the absence of such contrasting results.

2. It seems reasonable to me to "link" adjacent cohorts through an assumption that $F_9=F_{10}$ in a given year.

3. Isn't there any independent evidence (not presented in the report) for possible decline in "selectivity coefficient" or in "catchability" of fish older than age 11? The curves plotted for the two analysis methods (figure 5) are disturbingly different and it seems unlikely to me that one would see such a decline beginning at age 11 if the age of full maturity is age 9. In just two years after all fish are mature, they decide to become less vulnerable and live somewhere else? I'd sure like to see some additional evidence for this possibility.

4. The apparent agreement between cohort and catch-at-age analyses appears to be tied to pt. #1 above. I'm not impressed by the close agreement between the two methods; in fact, I'm disturbed by it! If the analysis methods are substantively different, they should give *different* results.

5. I'd like to see a maturation curve presented in the report. I am very concerned by the observation that 71% of the catch in 1986 was of fish less than age 9, and I didn't like the looks of the age compositon shifts depicted by Figure 3. Unless there is very substantial spawning activity among fish aged 5-7, it looks to me that there may be serious problems with spawning stock (see

pt #7). In the absence of the maturation curve, I couldn't judge.

6. How long do these fish live? I was greatly impressed with the continued "pile-up" of fish older than age 13 (Table 6). This could be added to the report in a single sentence.

7. Table 7 presents estimates of spawning stock from 1980 through 1987 or 1988. For M=0.2 these suggest that spawning stock has decreased to about 28-32% of that in 1980, and for M=0.15 to about 40-45% of spawning stock. Since the stock was not virgin in 1980 (1979 landings were ≈5,000 mt), this means that the real reduction in spawning stock has probably been greater than that indicated by the 1980-87/88 comparisons. In any event, current spawning stock could be as little as perhaps 20-25% of virgin spawning stock and probably no more than 40%. If such a reduced spawning stock were noted for other groundfish stocks, would there be an expression of concern?

8. I know that it's old hat, but I would have liked to have seen a surplus production model used for comparison. Just out of curiosity, I'd like to know what the recommended % of virgin biomass for MSY would be to compare with these other analyses.

9. I agree that some large cohorts (1977-1980) have been moving through the population and should improve numbers of older fully-mature fish in the near future.

10. The relative stability of landings from 1983 through 1986, coupled with the "timely" appearance of several strong year-classes suggests no immediate cause for panic, but I agree with the suggestion that yields in the years beyond 1990 may have to be seriously curtailed when compared to the proposed ABC.

11. If this is any indication of Hightower's work, the GMT will be have a good new leader to replace Bill Lenarz!!

## Appendix II. Sensitivity analysis of catch-at-age analysis (CAGEAN)

The difference in results from cohort and catch-at-age analysis illustrates the need for auxiliary information that would stabilize our estimates of current stock size. Because of the nature of the widow rockfish fishery, however, we have few potential sources of auxiliary information. Surveys of adult widow rockfish have not been attempted because of the high cost of sampling a midwater species with a highly contagious distribution. A midwater trawl survey of juvenile rockfish was begun in 1983 so the first surveyed year class will enter the fishery in 1988. If the survey is continued, the information it produces should be helpful in a few years. At present, our only source of auxiliary information is a four-year series of logbook data for the Oregon midwater trawl fleet. (The logbook data were obtained after the original assessment was completed). The strength of the relationship between logbook estimates of catch-per-unit-effort and fishing mortality rates is unknown. For that reason, we did not feel confident in forcing the CAGEAN model to mimic the pattern indicated by the logbook data. Instead, we used CAGEAN to establish the range of solutions consistent with the catch data, then compared the assessment results with the logbook data.

Our objective was to evaluate the sensitivity of the catch-at-age analysis to random sampling errors, as well as to changes in the assumptions used in the analysis. To evaluate the effect of sampling errors, we generated random catch matrices from the observed 1980-1987 catch-at-age matrix by adding a random error to each catch value. Thus, each replicate catch-at-age matrix represented a random perturbation of the observed data. Analyses by Sen (1984) indicated that the coefficient of variation (CV) for the mean number of widow rockfish per 50-pound cluster by sex and age class ranged from 12 to 24 percent in 1981 samples. Sen presented results only for those ages with CVs ≤ 25%; less commonly occurring age groups would have higher CVs. More recent unpublished analyses suggest that current CVs are lower than the 1981 estimates Sen obtained. We assumed a CV of 20% for all age groups in order to estimate the probable upper bound for the impact of sampling error on the assessment.

We produced a set of 100 replicate catch-at-age matrices for each of four assumptions about the ages at which selectivity is assumed equal to 1.0: age 10 only (s[10]=1.0), ages 9-10, ages 10-11, and ages 9-11. We also examined a fifth case with s[10]=1.0 but a starting F of 0.30 (instead of 0.25). The starting F is used in a preliminary cohort analysis that generates starting parameter estimates for the least-squares nonlinear fit. The analyses were done using a natural mortality rate (M) of 0.15. We believe that our conclusions from the sensitivity analysis would not change if the higher level of M (0.20) was used.

As in the assessment, we used average 1980-1987 Fs from cohort analysis as the "effort" data required by CAGEAN. We also used the same low weight (lambda=0.01) for the "effort" data, in order to obtain results that were relatively independent of the cohort analysis. The 1984-1987 annual Fs produced by CAGEAN were compared to estimates of total hours trawled, which were generated as follows. Logbook data from Oregon midwater trawl vessels (J. Golden, Oregon Dept. of Fish. and Wildlife, personal communication) provided estimates of 1984-1987 landings and hours trawled that were used to estimate catch per hour trawled (App. Table 1). Total landings for those years were divided by the catch rate estimates to provide an estimate of total effort. The estimate is based on the assumption that Oregon midwater trawl catch rates are representative of the coastwide rates.

## Results

Frequency distributions for estimated 1987 biomass (B[87]) were moderately sensitive to changes in the selectivity assumptions (App. Figure 1). We also observed a shift in the distribution when a higher starting F was used for the preliminary cohort analysis. The results did not appear to be less variable when more restrictive assumptions about selectivity were made. From 4-33% of the B[87] estimates were greater than 200,000 mt. In most instances, these estimates were obtained when recruitment increased over time and selectivity was high for the oldest (age-13+) fish. As App. Figure 2 illustrates for the s[10]=1.0 case, the extremely high B[87] estimates obtained for some of the replicates were due to recruitment estimates much higher than we believe possible (e.g., 1985 recruitment estimates of 1-2 billion fish, resulting in B[87] values of 1-5 million mt). When only the replicates with 1985 recruitment ≤ 100 million fish are plotted (App. Fig. 3), the results show that most recruitment estimates were less than 40 million fish and most estimates of s[13+] were relatively low (about 0.2-0.3).

Estimates of 1987 fishing mortality rates for age-10 fish (F[87]) varied in an inverse relationship with B[87] (App. Fig. 4). Even if B[87] values > 200,000 mt are excluded, F[87] still varied over a relatively wide range.

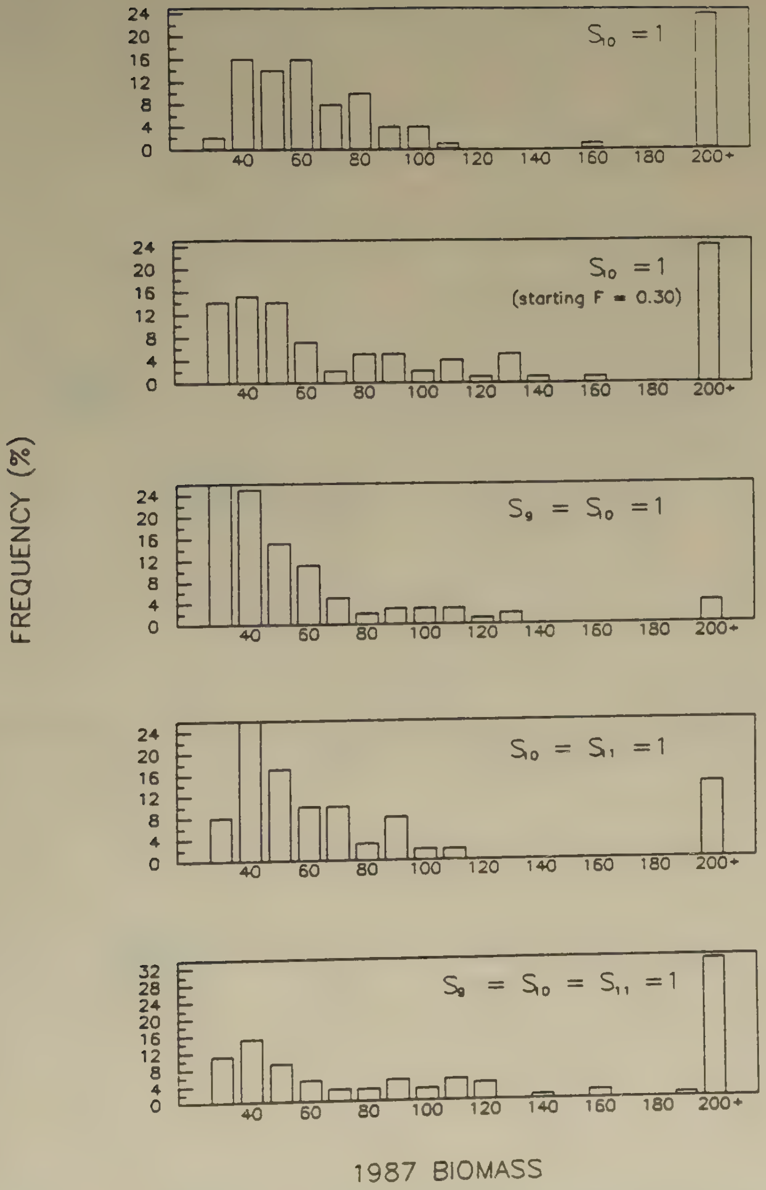
Correlations between 1984-1987 Fs and estimates of total hours trawled ranged from nearly -1 to 1 for the five cases we examined (App. Fig. 5). Large negative correlations were obtained when B[87] was large, because those were the instances where biomass increased from 1980-1987. Increasing biomass and relatively stable catches resulted in decreasing Fs over that interval, the opposite of the trend suggested by the effort data. Large positive correlations were obtained in those replicates where B[87] declined from 1980 to 1987, because the effort data are consistent with a substantial decline in stock size since the fishery began.

We draw several conclusions from these results:

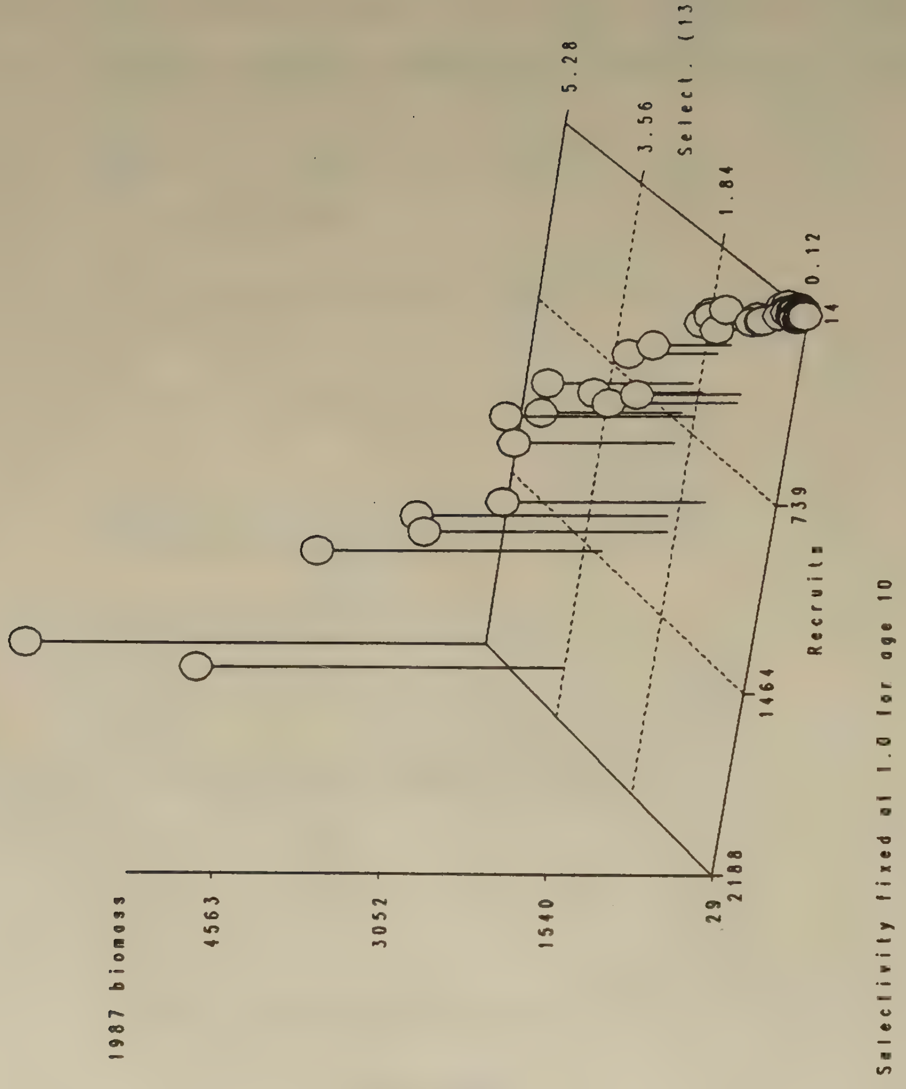
(1) A wide range of solutions is possible, given only an 8-year series of catch data and a low weight (lambda=0.01) applied to the "effort" data (cohort analysis F values) used in CAGEAN. These solutions include instances where stock size is increasing sharply in response to sharply increasing recruitment,

App. Table 1. Hours trawled, landings, and catch per hour trawled for the Oregon midwater trawl fleet from 1984-1987, and estimates of hours trawled coastwide (total coastwide landings divided by Oregon catch/hour trawled).

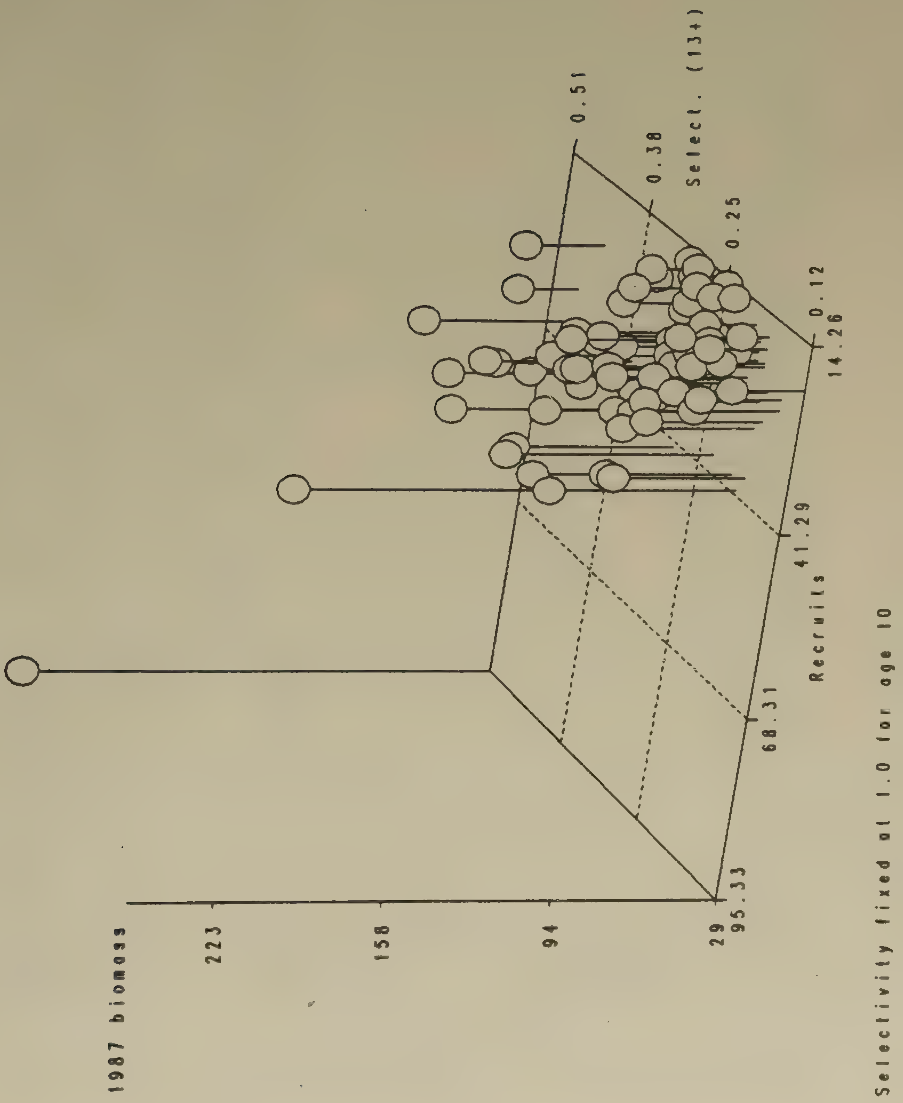
| Year | Hours trawled Oregon fleet | Landings Oregon fleet | Catch/hour trawled Oregon fleet | Estimated coastwide hour trawled |
|---|---|---|---|---|
| 1984 | 1,781 | 3,925 | 2.20 | 4,396 |
| 1985 | 2,227 | 3,425 | 1.54 | 5,751 |
| 1986 | 2,325 | 3,103 | 1.33 | 7,015 |
| 1987 | 3,103 | 5,102 | 1.64 | 7,430 |



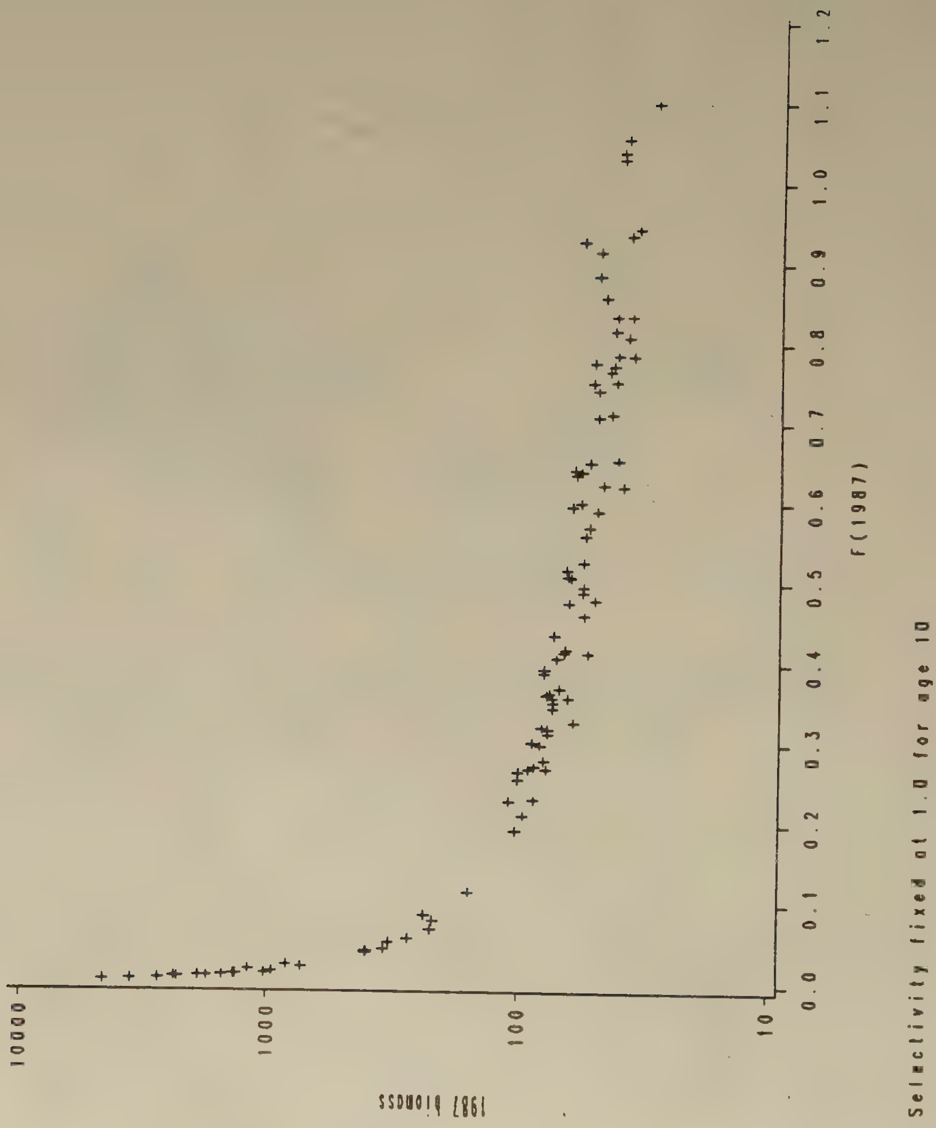
**App. Figure 1.** Frequency distributions for estimates of 1987 widow rockfish biomass (ages 5+), based on catch-at-age analysis of 100 randomly generated catch matrices. Four assumptions were examined regarding the ages at which selectivity was assumed equal to 1.0: age 10 only (cases 1-2); ages 9-10; ages 10-11; and ages 9-11. The starting F for the preliminary cohort analysis was 0.25 except in case 2, where 0.30 was used.



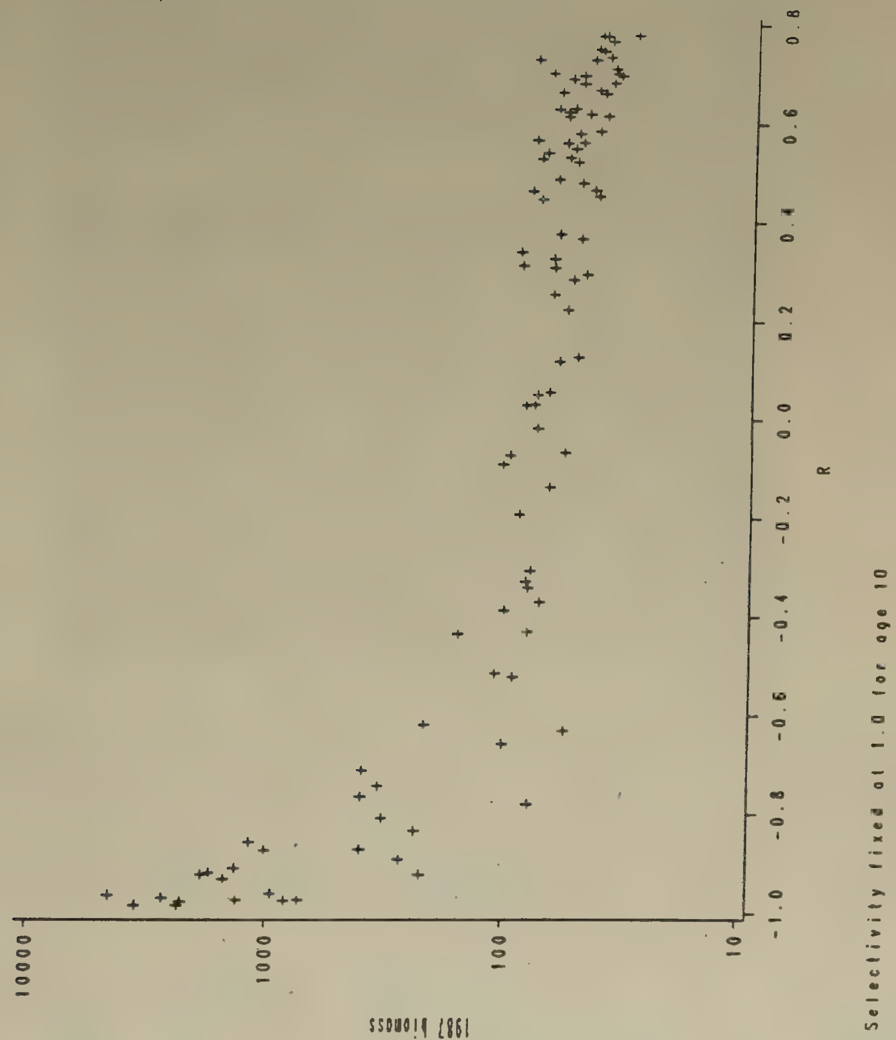
App. Figure 2. One-hundred replicate estimates of 1987 widow rockfish biomass versus number of 1985 age-5 recruits and relative selectivity at ages 13+, for the case where selectivity at age 10 is assumed to be 1.0.



**App. Figure 3.** Estimates of 1987 widow rockfish biomass versus number of 1985 age-5 recruits and relative selectivity at ages 13+, for the case where selectivity at age 10 is assumed to be 1.0. Only those replicates where recruitment was ≤ 100 million fish were plotted.



App. Figure 4. One-hundred replicate estimates of 1987 widow rockfish biomass versus the 1987 fishing mortality rate for age-10 fish, for the case where selectivity at age 10 is assumed to be 1.0. The relationship was similar for the other selectivity assumptions.

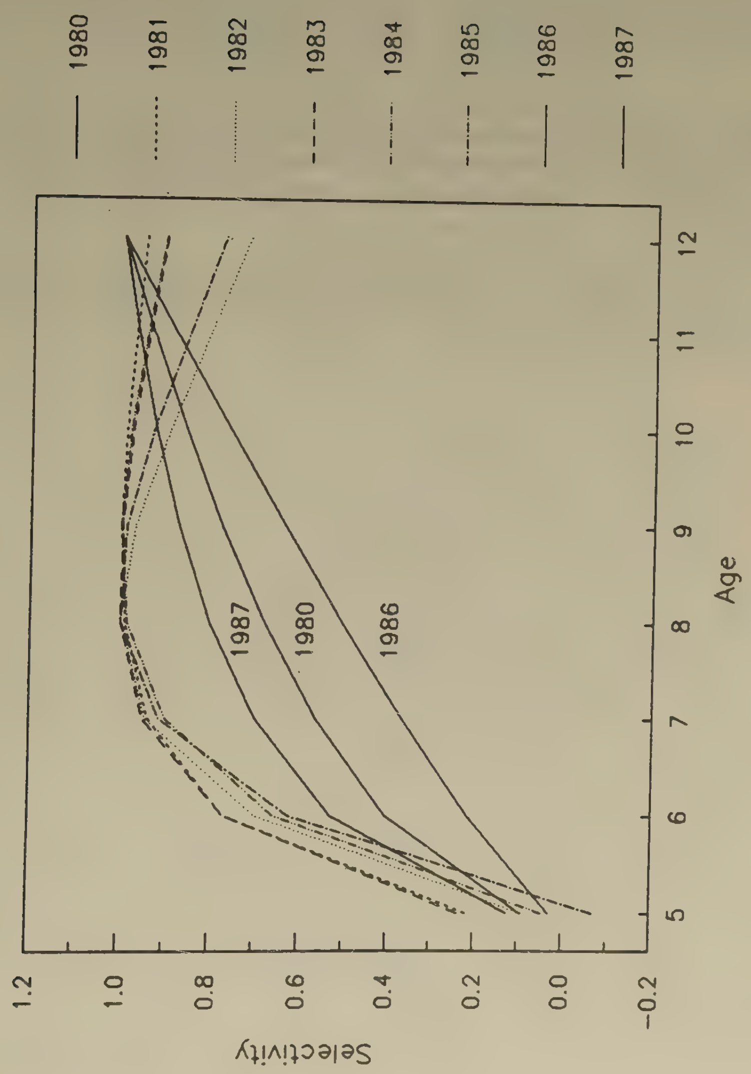


**App. Figure 5.** One-hundred replicate estimates of 1987 widow rockfish biomass versus the correlation between hours trawled (based on Oregon logbook data) and 1984-1987 fishing mortality rates for age-10 fish, for the case where selectivity at age 10 is assumed to be 1.0. The relationship was similar for the other selectivity assumptions.

> as well as a large number of cases indicating a relatively low current stock size. A more restricted set of solutions could be obtained by increasing lambda; however, forcing the least-squares model to reproduce the cohort analysis results will not provide much additional understanding. We prefer instead to use CAGEAN as a relatively independent estimate of current stock size.
>
> (2) If we assume that stock size has declined since the fishery began in 1980 (ruling out the cases where B[87] ≥ 200,000 mt), then most of the replicate analyses indicate that B[87] is between 25,000 and 75,000 mt.
>
> (3) If we assume that the correlation between 1984-1987 F and hours trawled should be greater than zero, then results from all five cases indicate that B[87] is probably less than 70,000 mt. The assumption that F and hours trawled are highly correlated may be inappropriate, given that our measure of effort excludes search time, changes in the level of experience for fishermen, and changes in gear technology. Catch-per-unit-effort for a schooling fish such as widow rockfish may not decline in proportion to the decline in stock size. For example, if school size is maintained but the number of schools declines, catch per tow could remain constant although increased search time would be required to locate schools.

Overall, we believe that results from the least-squares analysis support the conclusion that stock size has been reduced substantially since 1980. The results from cohort analysis, which suggest that B[87] is over 100,000 mt, are highly dependent on estimates of the size of the 1980 and 1981 year classes. Those estimates are unreliable because those year classes have been in the fishery for only 1-2 years and because those estimates are sensitive to changes in selectivity. Improved estimates will be possible after those year classes have been exploited for several years.

In addition, work is underway (R. Methot, Northwest and Alaska Fisheries Center) to develop an assessment model incorporating less restrictive assumptions about selectivity than CAGEAN. Results from cohort analysis indicate that the selectivity pattern for widow rockfish varied over time, perhaps due to changes in the spatial distribution of the fishery. We described the annual patterns by fitting three-parameter curves to the annual selectivity estimates from cohort analysis (App. Fig. 6). One of the assumptions required for CAGEAN is that the selectivity pattern does not change substantially over time. We do not know the impact of the changes depicted in App. Fig. 6. Residuals from catch-at-age analysis (using the



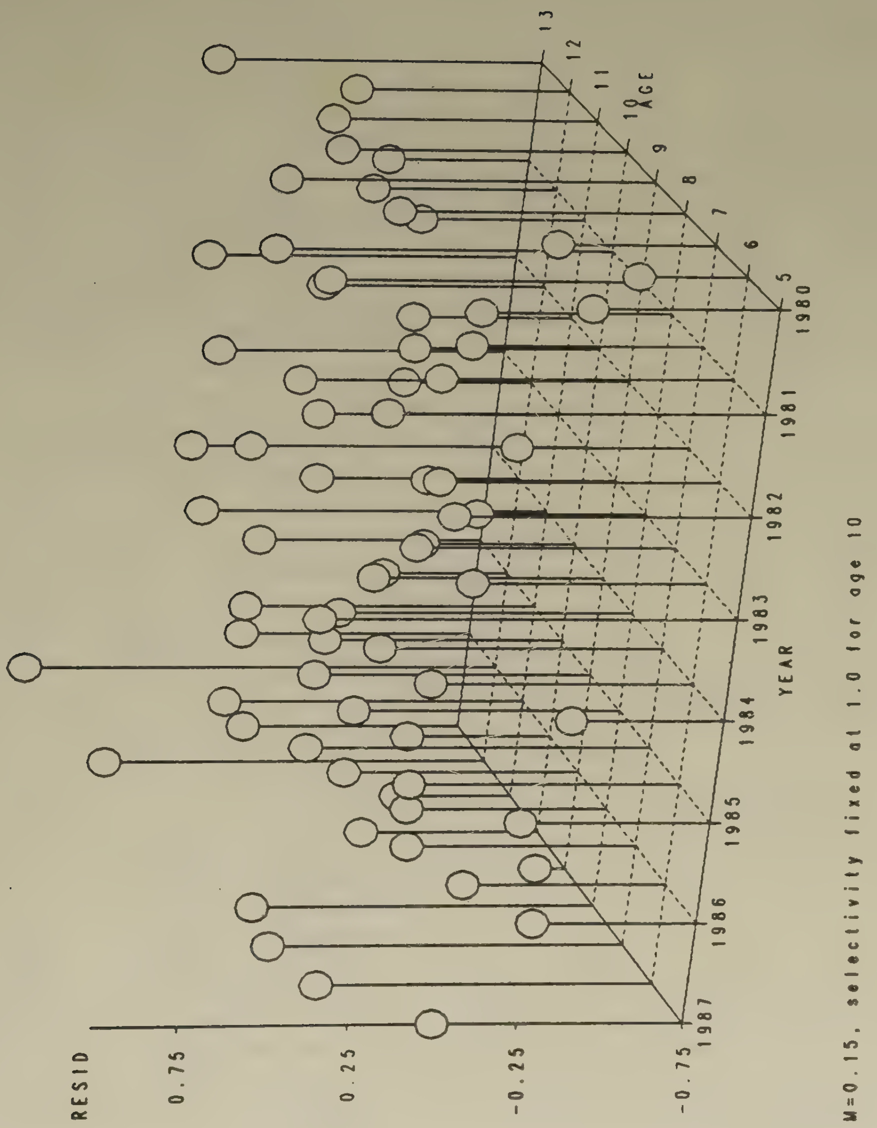
App. Figure 6. Predicted selectivity patterns for each year, obtained by fitting a three-parameter curve to the annual selectivity estimates from cohort analysis.

actual 1980-1987 catch data) do not show obvious trends (App. Fig. 7-8, App. Tables 2-3), although the 1987 catches from the 1980 and 1981 year classes are underrepresented by the model. It is possible to use CAGEAN to fit selectivity patterns separately for two or more time periods; however, we are reluctant to subdivide the already short data series.

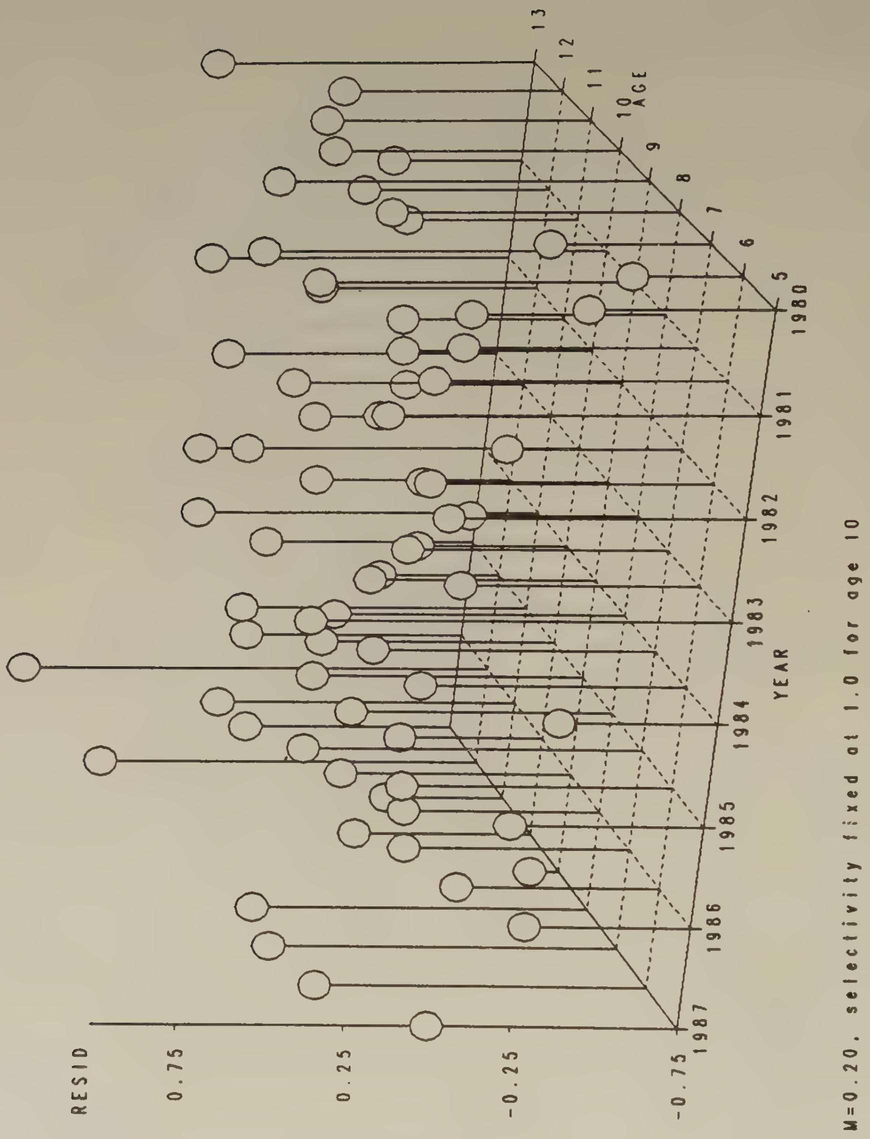
In summary, we feel that the apparent changes in selectivity lend support to our approach of using both cohort and catch-at-age analysis in the assessment. Until the additional data and improved assessment techniques are available, we believe a conservative harvesting policy (such as outlined in the assessment) is necessary.

## References

Sen, A. R. 1984. Sampling commercial rockfish landings in California. U. S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-45.



**App. Figure 7.** Residuals (log [observed catch] - log [predicted catch]) from the least-squares fit using CAGEAN to the 1980-1987 catch-at-age data, with M = 0.15.



App. Figure 8. Residuals (log [observed catch] - log [predicted catch]) from the least-squares fit using CAGEAN to the 1980-1987 catch-at-age data, with M = 0.20.

App. Table 2. Residuals (log(observed catch)-log(predicted catch)) from the least-squares fit using CAGEAN to the 1980-1987 catch-at-age data, with M=0.15.

| | | | | Year | | | | |
|---|---|---|---|---|---|---|---|---|
| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
| 5 | -.20635 | .34886 | .12045 | .47447 | -.30002 | -.18674 | -.26109 | .00021 |
| 6 | -.43148 | .11111 | .07846 | -.05579 | .03191 | .05920 | -.13792 | .26151 |
| 7 | -.27955 | -.06304 | -.23551 | .02702 | .09959 | .28543 | -.05440 | .32530 |
| 8 | .10520 | -.17633 | .06890 | -.23849 | .14092 | .06095 | -.13537 | .29618 |
| 9 | .35965 | .19432 | .24697 | -.17239 | -.04508 | .09991 | -.02593 | -.65503 |
| 10 | .11353 | .27553 | -.17917 | .28300 | -.27869 | -.01276 | -.30336 | -.19709 |
| 11 | .06043 | -.24482 | -.25899 | -.00294 | .32040 | .15278 | .18320 | -.38835 |
| 12 | -.09056 | -.18001 | -.06462 | -.35043 | -.11337 | -.35631 | .73128 | .44947 |
| 13+ | .25489 | -.30911 | .21357 | .14727 | .20232 | -.04815 | -.02615 | -.06360 |

App. Table 3. Residuals (log(observed catch)-log(predicted catch)) from the least-squares fit using CAGEAN to the 1980-1987 catch-at-age data, with M=0.20.

|  |  |  |  | Year |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| Age | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
| 5 | -.21470 | .33074 | .11453 | .48665 | -.28593 | -.17733 | -.25701 | -.00119 |
| 6 | -.42966 | .11144 | .08547 | -.04232 | .04141 | .06167 | -.13949 | .25513 |
| 7 | -.27715 | -.05923 | -.22930 | .03319 | .10192 | .27872 | -.06336 | .31456 |
| 8 | .11226 | -.16817 | .07281 | -.24147 | .13767 | .05129 | -.14628 | .28598 |
| 9 | .37136 | .21263 | .25421 | -.17949 | -.05276 | .09059 | -.03262 | -.66079 |
| 10 | .12202 | .30341 | -.16409 | .28133 | -.28354 | -.01792 | -.30091 | -.19182 |
| 11 | .06698 | -.21988 | -.24512 | -.00643 | .32130 | .15229 | .19264 | -.37388 |
| 12 | -.06744 | -.16689 | -.06959 | -.37662 | -.12758 | -.36535 | .73185 | .45517 |
| 13+ | .24991 | -.34280 | .19852 | .10966 | .16364 | -.08208 | -.05303 | -.08368 |

**UNITED STATES DEPARTMENT OF COMMERCE**
**National Oceanic and Atmospheric Administration**
NATIONAL MARINE FISHERIES SERVICE
Tiburon Laboratory
Southwest Fisheries Center
3150 Paradise Drive
Tiburon, California 94920

October 17, 1988 F/SWC3:JEH

MEMORANDUM FOR: James W. Glock
Pacific Fishery Management Council

FROM: F/SWC3 - Joseph E. Hightower J

SUBJECT: Supplemental Information Regarding 1988 Widow Rockfish Status of Stock Document

After further review of the draft widow rockfish status of stock document, Bill Lenarz and I discovered that the biomass at MSY (B[MSY]) estimates were incorrect. The values were based on the wrong fishing mortality rate; the correct values (Table A, enclosed) are moderately higher. The final version of the status of stock document contains the correct B[MSY] values.

Also enclosed are the two tables of biomass estimates that we discussed at the October meeting of the Groundfish Managment Team (Tables B-C). The table values represent estimates of the widow rockfish biomass that would be expected in years 1989-1993, assuming a constant harvest of 9,000 to 15,000 mt. The status of stock document contained the tables of fishing mortality rates (Table 10) that correspond to these biomass estimates. The biomass estimates are easier to interpret, however, so we wanted to make them available as well.

The two tables represent projections based on results from cohort and catch-at-age analysis. Estimates of current stock biomass differ considerably for the two approaches, and unfortunately, we have insufficient data to choose between the two sets of results. Our discussion at the GMT meeting focused on the catch-at-age analysis results because harvests that are acceptable for that more pessimistic case should not result in overfishing.

We concluded at the GMT meeting that, based on the catch-at-age analysis results, biomass would reach the MSY level within five years if a harvest of 11,000 or 12,000 mt. was maintained through 1992. For that reason, the GMT supported a 1989 ABC of 12,400 mt., which is the calculated value using the same ABC

Table a. Estimates of maximum sustainable yield (MSY) and biomass at MSY (B[MSY]) obtained from cohort and catch-at-age analysis at two levels of natural mortality (M) and using two assumptions about the stock-recruitment relationship.

| Assessment technique | M | Stock-recruitment relationship | Mean recruit. (millions) | MSY (000 mt) | B[MSY] (000 mt) |
|---|---|---|---|---|---|
| Cohort | 0.15 | Constant | 29.6 | 13.31 | 87.8 |
| | | Beverton-Holt | | 8.23 | 54.3 |
| | 0.20 | Constant | 34.2 | 12.66 | 83.3 |
| | | Beverton-Holt | | 8.61 | 56.6 |
| | Average | | | 10.7 | 70.5 |
| Catch-at-age | 0.15 | Constant | 20.8 | 8.64 | 66.1 |
| | | Beverton-Holt | | 5.93 | 45.4 |
| | 0.20 | Constant | 31.1 | 11.40 | 72.5 |
| | | Beverton-Holt | | 7.49 | 47.6 |
| | Average | | | 8.4 | 57.9 |

Table b. Estimates of widow rockfish biomass (ages 5+, thousands of metric tons (mt)) in 1989-1992 based on results of cohort analysis, assuming a constant harvest of 9,000 to 15,000 mt, a natural mortality rate (M) of 0.15 or 0.20, and one of three recruitment scenarios (mean observed recruitment, following the pattern observed in the juvenile rockfish survey, or following a Beverton-Holt stock recruitment curve).

| Target | | Mean observed | | Survey | | Beverton-Holt | | |
|---|---|---|---|---|---|---|---|---|
| harvest | Year | M=0.15 | M=0.20 | M=0.15 | M=0.20 | M=0.15 | M=0.20 | Average |
| 9,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 127.1 | 104.5 | 132.8 | 113.5 | 117.1 | 97.2 | 115.4 |
| | 1991 | 129.8 | 106.3 | 121.5 | 98.8 | 114.4 | 94.5 | 110.9 |
| | 1992 | 132.3 | 108.0 | 130.6 | 108.5 | 113.2 | 93.1 | 114.3 |
| | 1993 | 135.9 | 110.2 | 138.2 | 114.3 | 114.1 | 93.3 | 117.7 |
| 10,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 126.0 | 103.5 | 131.8 | 112.5 | 116.0 | 96.2 | 114.3 |
| | 1991 | 127.7 | 104.4 | 119.5 | 96.9 | 112.4 | 92.5 | 108.9 |
| | 1992 | 129.3 | 105.2 | 127.7 | 105.7 | 110.2 | 90.3 | 111.4 |
| | 1993 | 132.0 | 106.6 | 134.2 | 110.6 | 110.2 | 89.7 | 113.9 |
| 11,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 125.0 | 102.5 | 130.8 | 111.5 | 115.0 | 95.2 | 113.3 |
| | 1991 | 125.7 | 102.4 | 117.5 | 95.0 | 110.3 | 90.6 | 106.9 |
| | 1992 | 126.4 | 102.4 | 124.8 | 103.0 | 107.2 | 87.6 | 108.6 |
| | 1993 | 128.1 | 102.9 | 130.2 | 106.9 | 106.3 | 86.1 | 110.1 |
| 12,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 123.9 | 101.4 | 129.7 | 110.5 | 113.9 | 94.2 | 112.3 |
| | 1991 | 123.7 | 100.5 | 115.5 | 93.1 | 108.3 | 88.6 | 105.0 |
| | 1992 | 123.4 | 99.6 | 121.8 | 100.2 | 104.3 | 84.8 | 105.7 |
| | 1993 | 124.1 | 99.3 | 126.3 | 103.2 | 102.4 | 82.5 | 106.3 |
| 13,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 122.9 | 100.4 | 128.7 | 109.5 | 112.9 | 93.2 | 111.3 |
| | 1991 | 121.6 | 98.5 | 113.5 | 91.2 | 106.3 | 86.7 | 103.0 |
| | 1992 | 120.4 | 96.8 | 118.9 | 97.4 | 101.3 | 82.0 | 102.8 |
| | 1993 | 120.2 | 95.7 | 122.3 | 99.5 | 98.5 | 78.9 | 102.5 |
| 14,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 121.9 | 99.4 | 127.7 | 108.5 | 111.9 | 92.2 | 110.3 |
| | 1991 | 119.6 | 96.6 | 111.5 | 89.3 | 104.3 | 84.7 | 101.0 |
| | 1992 | 117.4 | 94.0 | 116.0 | 94.7 | 98.4 | 79.2 | 100.0 |
| | 1993 | 116.3 | 92.1 | 118.3 | 95.7 | 94.6 | 75.2 | 98.7 |
| 15,000 | 1989 | 124.1 | 103.0 | 101.3 | 77.7 | 117.5 | 98.2 | 103.6 |
| | 1990 | 120.8 | 98.4 | 126.6 | 107.5 | 110.8 | 91.1 | 109.2 |
| | 1991 | 117.6 | 94.6 | 109.5 | 87.4 | 102.2 | 82.8 | 99.0 |
| | 1992 | 114.4 | 91.2 | 113.0 | 91.9 | 95.4 | 76.4 | 97.1 |
| | 1993 | 112.3 | 88.4 | 114.3 | 92.0 | 90.6 | 71.6 | 94.9 |

Table c. Estimates of widow rockfish biomass (ages 5+, thousands of metric tons (mt)) in 1989-1992 based on results of catch-at-age analysis, assuming a constant harvest of 9,000 to 15,000 mt, a natural mortality rate (M) of 0.15 or 0.20, and one of three recruitment scenarios (mean observed recruitment, following the pattern observed in the juvenile rockfish survey, or following a Beverton-Holt stock recruitment curve).

| Target harvest | Year | Mean observed M=0.15 | Mean observed M=0.20 | Survey M=0.15 | Survey M=0.20 | Beverton-Holt M=0.15 | Beverton-Holt M=0.20 | Average |
|---|---|---|---|---|---|---|---|---|
| 9,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 58.4 | 70.2 | 63.2 | 78.5 | 55.2 | 71.4 | 66.2 |
| | 1991 | 58.0 | 72.4 | 53.2 | 66.1 | 53.2 | 73.8 | 62.8 |
| | 1992 | 57.6 | 74.5 | 57.5 | 75.4 | 51.2 | 75.7 | 65.3 |
| | 1993 | 57.5 | 76.6 | 59.3 | 80.2 | 49.1 | 77.1 | 66.6 |
| 10,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 57.4 | 69.2 | 62.2 | 77.6 | 54.2 | 70.4 | 65.2 |
| | 1991 | 55.9 | 70.4 | 51.2 | 64.1 | 51.2 | 71.8 | 60.8 |
| | 1992 | 54.6 | 71.6 | 54.5 | 72.6 | 48.2 | 72.8 | 62.4 |
| | 1993 | 53.5 | 72.9 | 55.2 | 76.4 | 45.2 | 73.4 | 62.8 |
| 11,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 56.4 | 68.2 | 61.1 | 76.6 | 53.2 | 69.4 | 64.2 |
| | 1991 | 53.9 | 68.4 | 49.2 | 62.2 | 49.1 | 69.8 | 58.8 |
| | 1992 | 51.5 | 68.7 | 51.6 | 69.8 | 45.1 | 70.0 | 59.5 |
| | 1993 | 49.5 | 69.2 | 51.1 | 72.6 | 41.2 | 69.7 | 58.9 |
| 12,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 55.3 | 67.2 | 60.1 | 75.6 | 52.1 | 68.4 | 63.1 |
| | 1991 | 51.8 | 66.5 | 47.2 | 60.3 | 47.1 | 67.8 | 56.8 |
| | 1992 | 48.5 | 65.9 | 48.6 | 67.1 | 42.1 | 67.1 | 56.5 |
| | 1993 | 45.5 | 65.5 | 46.9 | 68.8 | 37.2 | 66.0 | 55.0 |
| 13,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 54.3 | 66.2 | 59.1 | 74.6 | 51.1 | 67.4 | 62.1 |
| | 1991 | 49.8 | 64.5 | 45.2 | 58.4 | 45.0 | 65.9 | 54.8 |
| | 1992 | 45.5 | 63.0 | 45.7 | 64.3 | 39.1 | 64.2 | 53.6 |
| | 1993 | 41.5 | 61.9 | 42.8 | 64.9 | 33.3 | 62.3 | 51.1 |
| 14,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 53.3 | 65.2 | 58.1 | 73.6 | 50.1 | 66.4 | 61.1 |
| | 1991 | 47.7 | 62.5 | 43.2 | 56.5 | 43.0 | 63.9 | 52.8 |
| | 1992 | 42.4 | 60.1 | 42.7 | 61.5 | 36.1 | 61.4 | 50.7 |
| | 1993 | 37.5 | 58.1 | 38.7 | 61.1 | 29.3 | 58.6 | 47.2 |
| 15,000 | 1989 | 59.8 | 69.1 | 44.4 | 46.1 | 57.9 | 69.7 | 57.8 |
| | 1990 | 52.3 | 64.2 | 57.1 | 72.6 | 49.1 | 65.4 | 60.1 |
| | 1991 | 45.7 | 60.5 | 41.2 | 54.6 | 41.0 | 61.9 | 50.8 |
| | 1992 | 39.4 | 57.3 | 39.7 | 58.7 | 33.1 | 58.5 | 47.8 |
| | 1993 | 33.5 | 54.4 | 34.6 | 57.3 | 25.3 | 54.9 | 43.3 |

algorithm as in previous widow rockfish assessments. Based on the correct value of B[MSY] (57,900 mt), it appears that biomass in 1989 (57,800 mt) is at the MSY level, but should remain close to that level through 1992 at harvest levels of 11,000-12,000 mt. The GMT reviewed the corrected B[MSY] estimates and biomass projections and believes that a 12,400 mt. ABC for 1989 is still appropriate. ABC estimates for 1990 and beyond will be reevaluated annually as additional data become available.

Please contact me at (415) 556-0565 if you have questions or comments.

Enclosures